ASSESSING THE ROLE OF MACRO- AND MICROCLIMATE ON HOLM OAK PERFORMANCE IN MEDITERRANEAN DRYLANDS

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Abstract

Mediterranean drylands are expected to become drier due to climate change. This may aggravate desertification by increasing dryland susceptibility to land degradation, leading to the loss of biodiversity and ability to provide ecosystem services. In Mediterranean Basin drylands, a large area is occupied by oak woodlands, a semi-natural agro-silvopastoral system called *Montado* in Portugal. In the drier areas, where *Montado* seems to act as a buffer against desertification, the dominant tree species is Holm oak (*Quercus ilex* subsp. *rotundifolia*), However, in the last decades, a declining trend has been reported for Holm oak woodlands, mostly attributed to unsustainable land management, biotic factors and to an increase in aridity at a regional scale. Also, at a local scale, it has been shown that microclimate conditions driven by topography have a major influence on this species natural regeneration rates. Over the last decades, many (re)afforestation with Holm oak have been implemented to revert *Montado's* decline and combat desertification, although not always successful.

The aim of this work was to study the effect of macro- and microclimate on Holm oak performance, specifically on acorn germination and first summer seedling survival. Holm oak acorns were collected along a climatic gradient based on long-term precipitation (30 yrs.), resulting in 6 macroclimate provenances. In 2 sites, the driest and the wettest sites of the gradient, areas with contrasting microclimates were selected using Potential Solar Radiation (PSR) as a proxy of microclimate conditions. Holm oak performance was, thus, studied along a macroclimate gradient and in microclimate contrasting conditions.

Holm oak acorns from each provenance where characterized biometrically and acorn production evaluated. Germination of acorns and seedling survival were evaluated under greenhouse similar conditions and in the field under contrasting macro- and microclimate conditions.

We found that macro- and microclimatic provenance influences acorn size and germination. Drier sites and more exposed areas (higher PSR) had bigger acorns with higher germination. Field conditions did not seem to affect germination but rather the first summer seedling survival. The survival of Holm oak seedlings to the first summer was significantly higher in the wetter site and in less exposed areas than in the drier site and in more exposed areas.

This work provides guidelines to increase Holm oak seedling quantity and quality in nurseries to be used in (re)afforestation plans and to improve Holm oak young seedling survival, either by focusing (re)afforestation in microclimatic favorable areas (using remote sensing derived information like PSR), or by providing additional assistance to seedlings growing in drier and/or more exposed areas. In addition, it may also help to better understand Holm oak seedling mortality and/or natural regeneration patterns. Hence, these findings may contribute to improve the success of Holm oak (re)afforestation as a critical restoration tool to combat desertification in Portuguese drylands, and revert Holm oak *Montado*'s decline, particularly under a climate change scenario.

Keywords: Afforestation; Climate Change; *Quercus ilex*; Seedling survival; Seed Provenance

Resumo

Devido às alterações climáticas, é esperado um aumento de aridez nas zonas áridas que aumentará a sua susceptibilidade à degradação do solo, agravando o processo de desertificação, que leva à perda de biodiversidade e da capacidade de fornecer serviços de ecossistema. Na Bacia do Mediterrâneo, uma grande parte das zonas áridas é dominada por quercíneas, num sistema agrosilvopastoril, chamado Montado (em Portugal). No extremo mais árido, a espécie de árvore dominante é a Azinheira (*Quercus ilex* susbsp. *rotundifolia)*. No entanto, nas últimas décadas, tem-se assistido a um declínio desde sistema, maioritariamente atribuído a um uso do solo insustentável, a factores bióticos e ao aumento da aridez à escala regional. A uma escala local, foi demonstrado que as condições microclimáticas geradas pela topografia influenciam a regeneração natural desta espécie. Por outro lado, nas últimas décadas, muitas reflorestações têm sido implementadas para reverter o declínio do Montado e combater a desertificação, embora, por vezes, com elevado insucesso.

O objectivo deste trabalho foi estudar o efeito do macro- e do microclima no desempenho da Azinheira, especificamente na sua germinação e sobrevivência durante o primeiro Verão. Foram recolhidas bolotas de Azinheira ao longo de um gradiente de precipitação (média de 30 anos), em 6 proveniências macroclimáticas. No local mais seco e no local mais húmido no gradiente, foram seleccionadas áreas com microclima contrastante utilizando a Radiação Potencial Solar (PSR – *Potential Solar Radiation*) como preditor de condições microclimáticas. O desempenho da Azinheira foi assim estudado para estas diferentes proveniências macroclimáticas e em diferentes condições microclimáticas.

Primeiro, caracterizaram-se biometricamente bolotas de Azinheira recolhidas em cada proveniência e a sua produção foi também avaliada. A germinação e sobrevivência foram avaliadas em condições controladas em estufa, e sob condições microclimáticas contrastantes no campo.

As proveniências macro- e microclimáticas influenciaram a dimensão das bolotas e a sua germinação. Bolotas recolhidas em locais mais secos e mais expostos (maior PSR) mostraram maior dimensão e percentagem de germinação. As condições de campo não afectaram significativamente a germinação, mas sim a sobrevivência. A sobrevivência de plântulas de Azinheira à primeira seca de Verão foi significativamente maior em locais mais húmidos e áreas menos expostas do que em locais mais secos e áreas mais expostas.

Este trabalho contribui para melhor compreender a mortalidade de plântulas de Azinheira e também os padrões de regeneração natural. Os seus resultados fornecem linhas orientadoras para, por exemplo, aumentar o número e a qualidade de plântulas de Azinheira em viveiros para serem utilizados em reflorestações, e para melhorar a sobrevivência de jovens Azinheiras, seja direccionando as reflorestações para áreas com microclimas favoráveis (utilizando informação remota como o PSR) ou mostrando onde é necessário fornecer assistência adicional às plântulas a crescer em condições mais secas/áreas mais expostas. Contribuem assim para melhorar o sucesso de reflorestações de Azinheira, uma ferramenta de restauro crítica no combate à desertificação nas zonas áridas em Portugal e reverter o declínio do Montado, particularmente num cenário de alterações climáticas.

Palavras-chave: Reflorestação; Alterações climáticas; *Quercus ilex*; Sobrevivência; Proveniência de semente

Resumo detalhado

As zonas áridas *sensu lato* são caracterizadas por uma disponibilidade de água limitada devido à baixa precipitação e a elevadas taxas de evaporação no solo. Estas áreas são classificadas como hiper-áridas, áridas, semiáridas e secas sub-húmidas, de acordo com o seu índice de aridez. No seu conjunto, são habitadas por um terço da população mundial e cobrem cerca de 41% do território terrestre. Os elevados níveis de aridez levam a uma baixa produtividade primária, tornando estas zonas susceptíveis à degradação do solo, que neste caso se designa por desertificação. A desertificação, por sua vez, pode levar à perda de biodiversidade, fertilidade do solo e de serviços de ecossistema. Devido às alterações climáticas e a acções antropogénicas, é esperado que este problema vá afectar uma maior área no futuro. Os cenários de alterações climáticas prevêem um decréscimo de precipitação de 0.3% por década em determinados sítios e o aumento da frequência de eventos extremos de precipitação concentrados noutros locais, afectando diferentes locais de diferentes formas. No entanto, prevê-se que, para as zonas áridas, as alterações climáticas conduzam a um aumento generalizado da aridez.

Na Bacia do Mediterrâneo as zonas áridas ocupam cerca de 67% da área. Especificamente em Portugal as zonas áridas encontram-se no sudoeste do país, onde o ecossistema predominante é o Montado (*Dehesa* em Espanhol). É um sistema geralmente agro-florestal semi-natural caracterizado por uma densidade de árvores variável. As espécies arbóreas predominantes no Montado são a Azinheira (*Quercus ilex* subsp. *rotundifolia*) e o Sobreiro (*Quercus suber*) podendo encontrar-se esparsas ou mais densas, acomodando diferentes usos do solo. Este sistema fornece vários serviços de ecossistema, como por exemplo serviços de provisionamento, regulação da água e culturais. No entanto, este sistema encontra-se em declínio, com elevada mortalidade de indivíduos adultos e baixa regeneração natural, levando a uma menor densidade de árvores. Acresce que a previsão de aumento da aridez devido às alterações climáticas que já se faz sentir no sul de Portugal, poderá agravar esta tendência de desertificação. Ao nível regional, as causas do declínio do Montado são atribuídas sobretudo a um uso do solo indevido e ao aumento da aridez. No entanto, à escala local, foi demonstrado que as condições microclimáticas têm uma grande influência nas taxas de regeneração natural, havendo maior regeneração natural da Azinheira em microclimas com menor exposição solar.

Para inverter esta tendência de declínio e mitigar a desertificação e a degradação do solo, têm vindo a ser implementadas nas últimas décadas várias reflorestações com Sobreiro e Azinheira, podendo melhorar de forma significativa a biodiversidade característica destes sistemas mediterrânicos dominados por quercíneas. Existe uma longa história de reflorestações realizadas com Azinheira nas zonas áridas do sul de Portugal, onde a espécie é dominante. Contudo, nem todas as reflorestações têm sucesso. Uma das principais causas apontadas paras este insucesso são as primeiras secas de Verão.

Tendo em conta a tendência de declínio relatada para o Montado, a susceptibilidade à desertificação das áreas semi-áridas, as evidências empíricas de um baixo sucesso das reflorestações de Azinheira e as previsões de aumento da aridez para Portugal, aliados ao desconhecimento sobre a forma como estes factores interagem, este trabalho pretendeu avaliar o efeito do clima no desempenho da Azinheira à escala regional (denominada "macroclima") e à escala local (denominada "microclima"). Neste contexto, foram abordadas as seguintes questões: 1) A germinação, a produção de bolotas e o

estabelecimento de plântulas de Azinheira variam entre diferentes proveniências e condições de crescimento macro- e microclimáticas? Quais as proveniências ou condições de crescimento com maior sucesso?; 2) O efeito da proveniência ou condições de crescimento microclimáticas no desempenho da Azinheira varia com o macroclima, isto é, existe interacção entre o micro e o macroclima?

O trabalho decorreu na região do Alentejo, em zonas de Montado dominado ou com presença de Azinheira (*Quercus ilex* subsp. *rotundifolia*). Para tal, foram seleccionados seis locais ao longo de um gradiente macroclimático, utilizando a precipitação anual média de 30 anos para caracterizar o macroclima. Quatro dos locais haviam sido seleccionados num projecto anterior, o *Desertwarning* (PTDC/AAC-CLI/104913/2008), e outros dois foram escolhidos por serem locais onde decorrem estudos científicos de longo termo (LTsER Montado), para os quais este trabalho também contribui gerando mais informação sobre o sistema.

Em cada local, foram amostradas bolotas de Azinheiras de várias árvores (N ≥ 5), em dois anos consecutivos, um seco e quente, e outro "normal", isto é, com valores de precipitação dentro da média de longo-prazo. No segundo ano de amostragem, foi adicionalmente estimada a produção de bolota produzida por árvore amostrada, para tentar complementar a informação relativa ao ano anterior. Parte das bolotas recolhidas foram colocadas a germinar em condições semelhantes numa estufa e outra parte em tabuleiros colocados no campo em condições climaticamente contrastantes. Cada conjunto de bolotas foi caracterizado biometricamente (peso, volume e peso específico).

Para compreender o efeito do microclima foram seleccionadas duas áreas com condições microclimáticas contrastantes - uma área mais exposta à radiação solar e outra menos exposta -, utilizando a radiação solar potencial (PSR) como indicador microclimático, nos dois locais adicionais onde decorrem estudos científicos de longo termo, que correspondem também aos locais mais húmido e mais árido. Nas duas áreas em cada um dos locais, foram também recolhidas bolotas, que foram também caracterizadas e colocadas a germinar em condições contrastantes, isto é, no microclima de origem e no oposto, e um terceiro grupo em condições controladas na estufa. Depois de avaliada a germinação, a sobrevivência das plântulas foi monitorizada durante o primeiro Verão, em condições de estufa, e em condições climaticamente contrastantes no campo, quer em tabuleiros com solo comercial, quer após transplante directo para o solo do local de destino, nos dois extremos do gradiente de precipitação.

A dimensão das bolotas variou ao longo do gradiente macroclimático avaliado, aumentando do local mais húmido para o mais seco, onde foram recolhidas bolotas maiores. Além disso, observou-se uma maior germinação das bolotas provenientes de locais mais secos (macroclima), isto é, das bolotas maiores, observando-se uma correlação positiva entre o peso da bolota e a sua percentagem de germinação. Foi encontrada uma ligeira relação negativa entre o número de bolotas produzido por árvore e o peso das mesmas, independentemente da proveniência.

A uma escala local, nos dois extremos macroclimáticos avaliados - o local mais seco e o local mais húmido - a proveniência microclimática também mostrou ter um efeito significativo no peso das bolotas e na respectiva germinação. O peso das bolotas e a sua germinação foi maior para bolotas provenientes de locais mais secos (macroclima) e de áreas mais expostas (microclima), do que para bolotas provindas das condições opostas. Verificou-se ainda um efeito mais marcado do microclima no peso e na germinação de bolotas no local mais seco, do que no local mais húmido, indicando a existência de uma interacção entre o micro e o macroclima.

Em relação à sobrevivência de plântulas de Azinheira à primeira seca de Verão, esta foi afectada sobretudo pelas condições macro- e microclimáticas em que se desenvolveram as plântulas, e não pela sua proveniência macro- ou microclimática, que não teve efeito significativo na sobrevivência. As plântulas a crescer no local mais húmido e em áreas com menor exposição solar (microclima mais favorável) tiveram uma maior sobrevivência após a primeira seca de Verão, do que as que se encontravam no local mais seco, e nas áreas mais expostas.

Em suma, com este trabalho concluiu-se que a proveniência macro- e microclimática das bolotas é importante para o peso da bolota e para a sua germinação, sendo que estes dois estão correlacionados positivamente. À luz destes resultados, a escolha de bolotas mais pesadas e/ou de proveniências climaticamente mais áridas poderá contribuir para aumentar a disponibilidade de plântulas de Azinheira em viveiros, para serem usadas em reflorestações. Pelo contrário, para a sobrevivência de plântulas de Azinheira à primeira seca de Verão tiveram um papel decisivo as condições macro- e microclimáticas em que a planta se desenvolveu no campo, e não a respectiva proveniência climática. Neste sentido, a utilização de informação microclimática baseada em modelos topográficos de detecção remota permite prever a sobrevivência de plântulas de Azinheira a uma escala local (p. ex. permitindo a distinção de diferentes zonas microclimáticas dentro de uma mesma propriedade), sendo um contributo importante para orientar decisões quanto ao uso do solo mais adequado em cada caso. Ao permitir mapear áreas onde a sobrevivência de plântulas de Azinheira ao primeiro Verão é provavelmente maior, revela assim áreas com um maior potencial para reflorestações bem-sucedidas e possivelmente, com maior potencial para a regeneração natural da espécie. Isto permite alocar fundos e meios, tanto para acções de arborização como de conservação (p. ex. criação de zonas de exclusão de pastoreio), em áreas estratégicas com menor custo e maior benefício, de forma mais eficiente. Assim, os resultados deste trabalho poderão contribuir para melhorar o sucesso de reflorestações de Azinheira, uma ferramenta crítica de restauro para combater a desertificação nas zonas mais áridas de Portugal, ou noutras zonas equivalentes, e reverter o declínio do Montado, particularmente num cenário de alterações climáticas.

Table of contents

Tables index

Figure index

Abbreviations List

ASW	Acorn specific weight
ASW15	Acorn specific weight of the 15 biggest acorns
AV	Acorn volume
AV15	Acorn volume of the 15 biggest acorns
AW	Acorn weight
AW15	Acorn weight of the 15 biggest acorns
DLD	Desertification and land degradation
FS	Field survival
GLM	Generalized linear model
GMa	Germination per macroclimate
GMi	Germination per microclimate
GS	Greenhouse survival
GT	Germination per tree
LTER	Long term ecological research site
MAP	Mean annual precipitation
MAPd	Mean annual precipitation – destination
MAPp	Mean annual precipitation – provenance
PSR	Potential Solar Radiation
PSRd	Potential solar radiation – destination
PSRp	Potential solar radiation – provenance
Fig. S	Supplementary Figure
Table S	Supplementary Table
SV	Sown acorns volume
SW	Sown acorns weight
yrs.	Years

1 – Introduction

1.1 – Drylands, desertification and climate change

Drylands are characterized by limited water availability due to low rainfall and high evaporation rates (Cherlet et al. 2018). These areas are classified as hyper-arid, arid, semi-arid and dry sub-humid, according to increasing values of the aridity index (Middleton and Thomas, 1992). Drylands are home to more than 1/3 of the world population and cover about 41% of all land surface (Reynolds et al. 2007).

High aridity levels in drylands limit primary productivity, making them highly susceptible to desertification, which is defined as land degradation occurring in drylands due to climate and anthropogenic activities (MEA 2005; Safriel 2009; Ashton 2012). Desertification leads to the loss of biodiversity, fertile land and many other ecosystem services (Reynolds et al. 2007). This problem already affects many dryland areas and is expected to worsen due to climate change and human activities (Cherlet et al. 2018). Climate change is expected to lead to a decrease in rainfall of 0.3% per decade in certain places and to increase the frequency of extreme events such as drought and heavy rainfall events in others, affecting particular places in different ways worldwide (IPCC 2014). However, climate change predictions point out to an increase in aridity in the near future within the dryland continuum (Cherlet et al. 2018; Koutroulis 2019).

1.2 – Mediterranean dryland oak woodlands

Drylands occupy about 67% of the Mediterranean Basin (White & Nackoney 2003). Specifically in Portugal, drylands are found mostly in the southern part of the country. Climate predictions for this region suggest an increase in aridity (Fig. 1) (Costa et al. 2008) and likely shifts in the distribution ranges of some plant species (Resco De Dios et al. 2007; Benito Garzón et al. 2008). Currently, the areas classified as semi-arid and dry-sub humid are largely occupied by oak woodlands, a system called *Montado* in Portugal (*Dehesa* in Spain). This system occupies 35% of the forest area *sensu lato* in Portugal (Instituto Nacional de Estatística 2019)

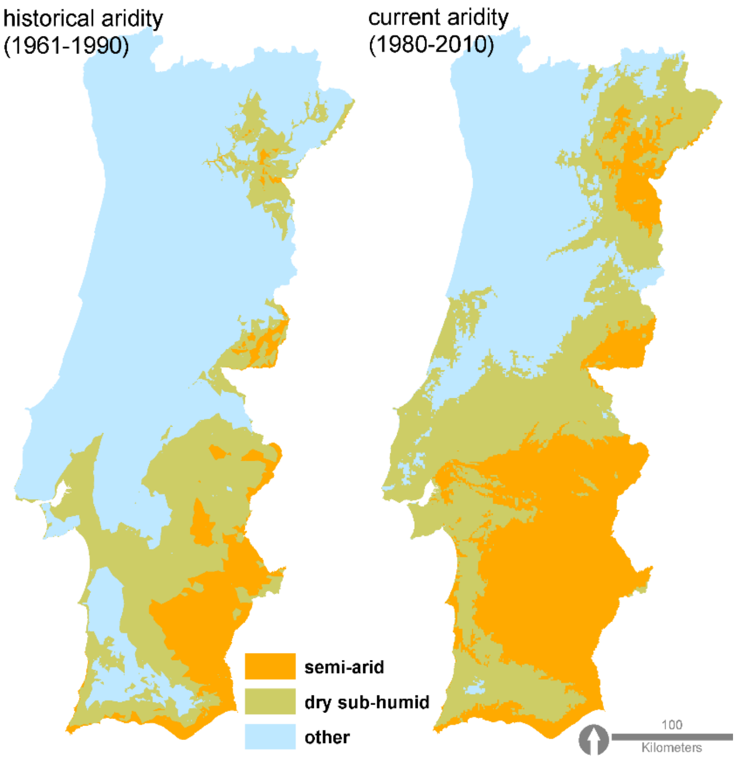

Figure 1. Aridity Index in continental Portugal – comparison between the averages of 1961-1990 and 180-2010. Source, personal communication: CNCD – Comissão Nacional de Combate à Desertificação, L. Rosário (2010)

Montado is a semi-natural ecosystem resulting from anthropogenic influence for centuries (Marañón 1988; Pinto-Correia et al. 2011). The dominant evergreen tree species are Holm oak (*Quercus ilex* subsp. *rotundifolia* Lam., syn *Quercus rotundifolia* Lam.) and Cork oak (*Quercus sub*er L.). The understory of these ecosystems is composed of semi-natural grasslands with some patches of shrubs. Within the Portuguese drylands, Holm oak is more common in the inland semi-arid areas, whereas Cork oak dominates in the dry-sub humid areas, closer to the Atlantic coast (Belo et al. 2009).

Montado systems provide a diversity of ecosystems services, such as soil conservation and formation, climate regulation, water and air renewal, carbon sequestration, pollination, provisioning services (e.g. cork; wood; livestock; food) as well as cultural heritage and identity, landscape and gastronomy (Bugalho et al. 2009; Sá-Sousa 2014). Hence, *Montados* are recognized as systems with high importance for both socio-economic reasons and nature conservation, being ranked as a High Nature Value (HNV) farmland (Cooper et al. 2007), allowing farming while maintaining a remarkably high biodiversity (da Silva et al. 2009; Godinho et al. 2011). However, for *Montado* to keep these characteristics, a moderate management is required. Indeed, intense land use such as overgrazing, as well as land abandonment due to rural depopulation, both lead to decreased biodiversity (Pinto-Correia 1993; Bugalho et al. 2011; Godinho et al. 2016).

1.3 – Oak woodlands' declining trend

In Portugal, previous works have reported a declining trend for oak woodlands (Pinto-Correia & Azeda 2017). Although it is not consensual if the system is decreasing in area (ICNF - Instituto para a Conservação da Natureza e Florestas 2019a; Muñoz-Rojas et al. 2019), it is clear that tree density is declining. Decline is the decrease in tree density due to adult tree mortality and insufficient natural regeneration (Benito Garzón et al. 2008; Sá-Sousa 2014; Muñoz-Rojas et al. 2019). At the landscape scale, *Montado* land degradation has been related to overgrazing and intensification of other types of land use (Godinho et al. 2016), as well as extreme climatic events (e.g. flooding followed by drought) and the presence of pathogenic agents (Benito Garzón et al. 2008; Corcobado et al. 2013; Pinto-Correia et al. 2013; Corcobado et al. 2014), which may increase tree mortality and prevent regeneration. In Portugal, areas with ≥ 10% Holm oak cover have decreased 10% from 1995 to 2010, while in the same time frame areas with < 10% Holm oak cover increased (ICNF - Instituto para a Conservação da Natureza e Florestas 2013a).

Holm oak decline, driven by pests and pathogenic agents as well as unsustainable management, will be aggravated by scenarios of increasing aridity (Costa et al. 2008; Corcobado et al. 2013; Godinho et al. 2016). In addition, at a local scale, microclimate conditions e.g. generated by topography, may greatly affect Holm oak natural regeneration over time (Príncipe et al. 2014). Using Potential Solar Radiation (PSR), this is, the solar energy that arrives to a certain area, as a proxy of microclimate conditions, Príncipe and co-authors (2014) found difference in Holm oak natural regeneration in different microclimate conditions. A much higher natural regeneration rate of Holm oak took place throughout the years in less exposed north-faced slopes with low PSR, than in south-facing more inhospitable slopes with a higher PSR. Accordingly, other works reported an influence of microclimatic conditions such as higher air and soil humidity and lower temperature, on acorn germination, leading to greater germination and higher seedling survival (Oliet et al. 2015).

1.4 – Holm oak (re)afforestation as a restoration tool

(Re)afforestation has been extensively used as a restoration tool to combat desertification in the Mediterranean Basin (Safriel 2009), and in Portugal in particular (DGRF 2006). Planted forests (Fig. 2) can provide over the long term many ecosystem services such as carbon sequestration, water and climate regulation, or biodiversity conservation (Belo et al. 2009; Mori et al. 2017), and can also contribute to soil protection and formation, helping to combat land degradation and adapt to climate change (DGRF 2006; ICNF - Instituto para a Conservação da Natureza e Florestas 2013b)

Figure 2. Holm oak (re)afforestation in southern Portugal

In Portugal, many (re)afforestation projects have been implemented since 1938, supported by different funding programs (Table 1).

The most common species used in reforestation plans in Portuguese drylands are Holm oak, Cork oak and Stone pine (*Pinus pinea,* L.) (Rey Benayas & Camacho-Cruz 2004; del Campo et al. 2009; Nunes et al. 2017). In drier areas, in particular, reforestation with Holm oak looks like a good option, since the species seems to be at its optimal distribution range (Surová et al. 2008). Yet, in 2010 more than 50% of Holm oak stands were in decline (Pinto-Correia et al. 2013). Nonetheless, from 2003 to 2018 only 1029 ha were approved for Holm oak (re)afforestation (1% of all (re)afforestation plans) (ICNF - Instituto para a Conservação da Natureza e Florestas 2019b). A low success of Holm oak (re)afforestation has been occasionally reported, e.g. by landowners, allegedly caused by several factors such as the presence of pathogenic agents, drought or aridity (Corcobado et al. 2013; Godinho et al. 2016; Colangelo et al. 2018). However, a comprehensive quantitative assessment of Holm oak (re)afforestation success in Portugal is lacking. A better understanding of the level and causes of failure over space and time could contribute decisively to the improvement of (re)afforestation plans and techniques, currently and under future climate scenarios.

Table 1. Financing programs for (re)afforestation (adapted from Nunes et al 2017). Source: (DGRF 2006)

Period	Funding source	(Re)afforested area
1938 - 1964	Plano de Povoamento Florestal	327 523 ha
1964 - 1983	Fundo de Fomento Florestal	126 934 ha
1981 - 1988	Projecto Florestal Português/Banco Mundial	131 908 ha
1988 - 1996	Programa de Acção Florestal (PAF)	325 344 ha
1991 - 1993	Regulamento (CEE) 2080/91	18 203 ha
1994 - 1999	Programa de Desenvolvimento Florestal (PAMAF)	226 262 ha
1994 - 1999	Regulamento (CEE) 2080/92	173 372 ha
2000 - 2006	AGRO	133 430 ha
2000 - 2006	RURIS	33 021 ha
2004 - on going	Fundo Florestal Permanente	...

1.5 – Limitations to Holm oak (re)afforestation success

(Re)afforestation of Holm oak are made with direct acorn sowing or by seedling transplant (Gonçalves et al. 2001; Carecho 2015; Oliet et al. 2015). Therefore, Holm oak establishment success at the initial stages, might be constrained by acorn germination and/or by seedling survival in the first years after sowing/plantation.

Acorns are described as recalcitrant seeds, not been able to be store for long periods of time, being at risk of desiccation. Dehydration of these seed takes place once the seeds are exposed to not ideal conditions of humidity and temperature for a period of time, early germination can occur (expose the radicle prematurely, compromising the seedling) or de-hydration of the acorn, leading to no germination success (Pasquini et al. 2011). Previous works have suggested the use of heavier acorns as a way to ensure high germination (Carecho 2015), highlighting the role of 'seed quality' for germination. Also, microclimatic conditions matter; low radiation and high relative humidity increase acorn germination (Broncano et al. 1998; Oliet et al. 2015). Under field conditions, acorn germination may be also undermined by predation, both pre and post-dispersion, by invertebrates and vertebrates respectively (Leiva & Fernández-Alés 2005; Muñoz et al. 2009).

Seedling survival in the field is highly constrained by the first summer drought (Ramón Vallejo et al. 2012), specifically for Holm oak (del Campo et al. 2009; Palacios et al. 2009; Puértolas et al. 2010). In the first years of establishment soil moisture is crucial for plant development (Oliet et al. 2015). Climatic extreme events, together with the presence of pathogenic agents, reduce Holm oak seedling survival (Corcobado et al. 2014). Hence, techniques such as summer irrigation or artificial protection from direct solar exposition, may increase plant survival (Rey Benayas & Camacho-Cruz 2004). At a local scale, seedling survival may depend also on microclimate conditions, which have been found to largely influence natural regeneration rate. In areas with lower solar exposition (e.g. driven by topography), Holm oak natural regeneration was higher and quicker than in areas with higher solar exposition (Príncipe et al. 2014). Holm oak survival may also depend on seed provenance; drier provenances showed a tendency to have a higher resistance to drought (Palacios et al. 2009; Andivia et al. 2018).

At later stages of establishment, for young and adult trees, other factors (e.g. climate, pathogens) may influence oak (re)afforestation success (Rey Benayas & Camacho-Cruz 2004; Smit et al. 2009). Yet, early-stages as seedling are often the most challenging for the establishment of these slow-growing species (Oliet et al. 2015). Hence, understanding early-stage limitations may greatly contribute to a more cost-effective (re)afforestation output.

1.6 – Objectives

Taking into consideration the declining trend reported for *Montado*, the susceptibility to desertification of the semi-arid areas where this ecosystem is dominant, empirical evidences or occasional report of Holm oak (re)afforestation low success, and climate change predictions for Portugal, as well as knowledge gaps on how these factors interact, this work will address the effect of climate on Holm oak performance, at a regional scale (hereafter called “macroclimate”), and at a local scale (hereafter called “microclimate”). The following research questions will be addressed:

1. Does macroclimate influence acorn germination and seedling establishment? We hypothesized that acorns collected from, or growing in drier sites, will show lower germination and seedling establishment, than those from wetter sites.

2. Do local microclimatic conditions influence acorn germination and seedling establishment? We hypothesized that acorns collected from or growing in more favorable microclimatic conditions with low Potential Solar Radiation (PSR), will show higher germination and seedling establishment, than those from unfavorable microclimatic conditions (high PSR).

3. Is there an interaction between microclimate and macroclimate? We hypothesized that microclimate conditions will have a greater influence on Holm oak germination and establishment in drier sites, than in wetter sites.

2 – Methods

2.1 – Study Area

This work took place in the region of Baixo Alentejo, Portugal. This area represents a large part of dryland ecosystems in Portugal, encompassing a gradient of increasing aridity that goes from dry sub-humid to semi-arid areas, from northwest/coast towards southeast/inland. The region of Baixo Alentejo is mostly occupied by oak woodlands, called *Montado* in Portugal, and *Dehesa* in Spain. These semi-natural savanna-like oak woodlands with scattered trees have been modeled by agro-silvo-pastoral human activities for a long time. The dominant arboreal species are evergreen oaks, namely Cork oak (*Quercus suber*) in less arid areas, while Holm oak (*Quercus ilex* subs. *rotundifolia)* dominates in drier areas. This study focuses specifically on Holm oak woodlands (Fig 3). The understory of these ecosystems is composed of semi-natural grasslands with some patches of shrubs. Generally, the soil of these areas is shallow and poor, classified as lithosoils. Mean annual precipitation ranges from 520mm to 632mm (50 yrs.) along the study area, with high inter-annual variability.

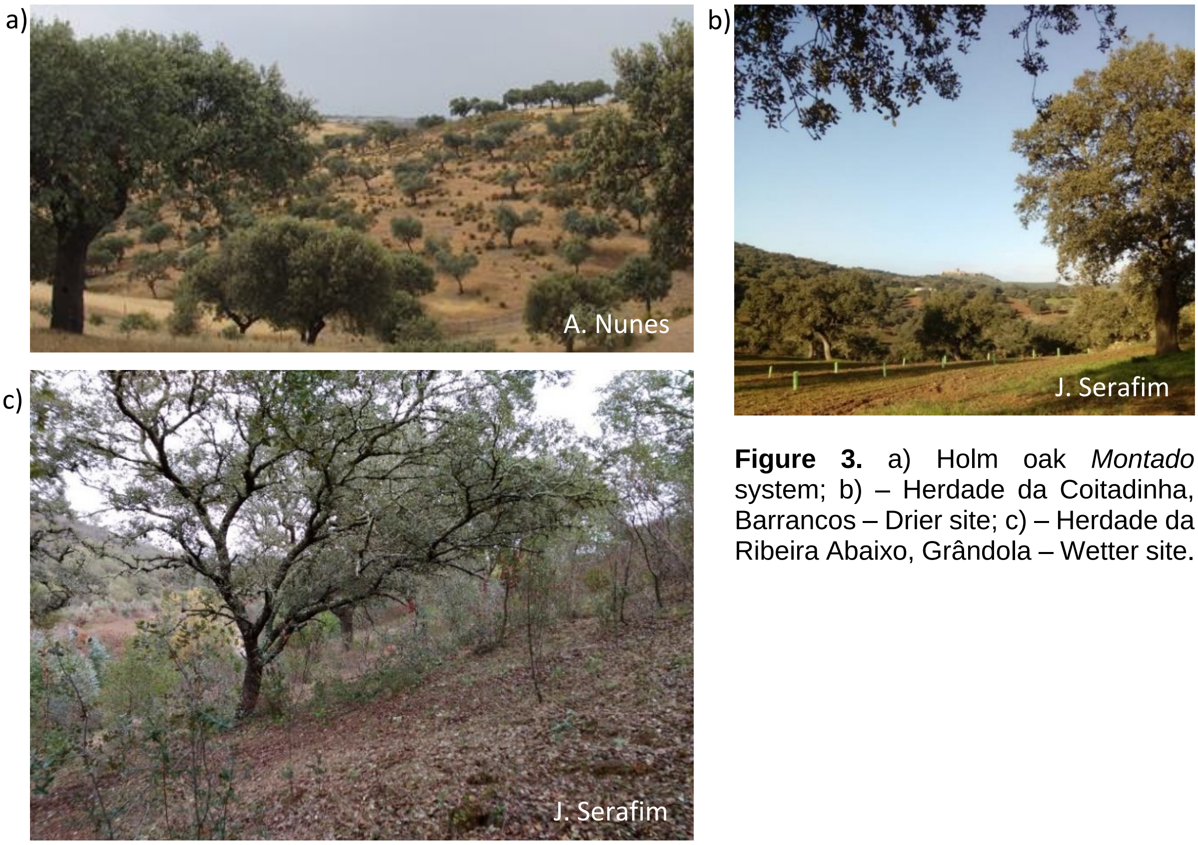

Figure 3. a) Holm oak *Montado* system; b) – Herdade da Coitadinha, Barrancos – Drier site; c) – Herdade da Ribeira Abaixo, Grândola – Wetter site.

2.2 – Experimental design and data collection

This work involved assessing the effect of climate at a regional scale (hereafter called "macroclimate") and at a local scale (hereafter called "microclimate") on Holm oak germination and establishment. A summary of the predictors and the tests performed can be found in Table 1. To study the effect of macroclimate, Holm oak acorns were collected from different macroclimate provenances in sites distributed along an aridity gradient, and their germination and seedling survival were compared under similar (greenhouse) and contrasting (field) conditions (Table 1; see section 2.2.1 for a detailed description). The effect of microclimate was tested in the field, comparing Holm oak acorn germination and seedling survival under two contrasting microclimates, within two sites with contrasting aridity values at the extremes of the macroclimatic gradient – a drier site and a wetter site (Fig. 3b-c). Therefore, the effects of microclimate were tested not only *per se*, but also in interaction with macroclimate (Table 1; see section 2.2.2 for a detailed description).

Table 2. Summary of the predictors tested and the responses evaluated.

Predictors		Test on	Response
Macroclimate	Six different provenances	Acorn provenance	Acorn production
			Acorn germination (under similar conditions)
			Seedling survival after 1st summer (under similar conditions)
		Acorn provenance x contrasting field conditions	Transplanted seedling survival after 1st summer (under field conditions)
Microclimate x Macroclimate	Two contrasting microclimates in two extremes of aridity	Acorn provenance	Acorn production (field)
			Acorn germination (under similar conditions)
			Seedling survival after 1st summer (under similar conditions)
		Acorn provenance x contrasting field conditions	Acorn germination (under different conditions)
			Transplanted seedling survival after 1st summer (under field conditions)

The sampling of acorns took place in the autumn of 2017 and 2018 (further detailed in 2.2.3). Overall, the year of 2017 was considered extremely hot and dry compared to the long-term average (hereafter called "dry year"), having the second higher average temperature since 1931, and the highest mean maximum temperature within the same period (IPMA 2018). The year 2017 was considered also one of the driest of the previous decades, being the fifth with the lowest mean annual precipitation, 541 mm, and the third with the lowest annual rainfall amount since 1931 (IPMA 2018).

On the other hand, the year of 2018 was considered an average year (hereafter called "normal year"), with the mean temperature and precipitation similar to the long-term annual means, nonetheless, being slightly warmer than the average since 1971 (IPMA 2019). The mean annual precipitation was 940 mm, almost the double of the previous year (IPMA 2019). Sampling was done in two consecutive years to account for inter-annual climatic variability and its potential effect on Holm oak response.

2.2.1 – Testing the effect of macroclimate provenance

For this study, the 30-years mean annual precipitation (1960-1990) was used as a proxy of macroclimate, retrieved from Worldclim database (Hijmans et al. 2005). Six different sites occupied by Holm oak woodlands were selected along a climatic gradient covering the range of precipitation of the study area (Fig. 4.a). Four of these sites were previously selected from the project *Desertwarning* (PTDC/AAC-CLI/104913/2008). Two additional sites were chosen, to enlarge the range of precipitation covered by the current study, and because they integrate the LTsER Montado platform – Long Term Ecological Research Sites (http://www.ltsermontado.pt/), taking advantage of other research works are being developed, which may help the interpretation of the results obtained. These two LTsER sites represent the extremes (drier and wetter) of the aridity levels found in Baixo Alentejo (Fig. 6i-ii; Fig. 8i-ii).

In each of the six sites selected along the macroclimate gradient, Holm oak acorns were collected in two sampling periods according to section 2.2.3.. Long-term mean annual precipitation was extracted from Worldclim database (http://www.worldclim.org/) with a 30 arc-seconds (~1 km^2) resolution (Hijmans et al. 2005). Acorns from different macroclimate provenances (35 acorns per site in 2017; 25 acorns per site in 2018) were taken to the lab and their fresh weight was measured (see section 2.2.3 for more details). Some days after, they were set to germinate under similar conditions in germination trays (6x6x16cm) in the greenhouse in Faculty of Sciences of the University of Lisbon, subject to local external environmental conditions, without temperature control (Fig. 4b). The soil used in trays was a commercial peat soil (Substrato especial Germinação, SIRO). Trays were watered every 2 weeks, from winter to early spring. It was considered as germination once the seedling emerged from the soil. In the middle of spring, after seedling emergence, seedlings were moved out of the greenhouse and were watered weekly (Fig. 5.a-b). This was done in 2017 and repeated in 2018.

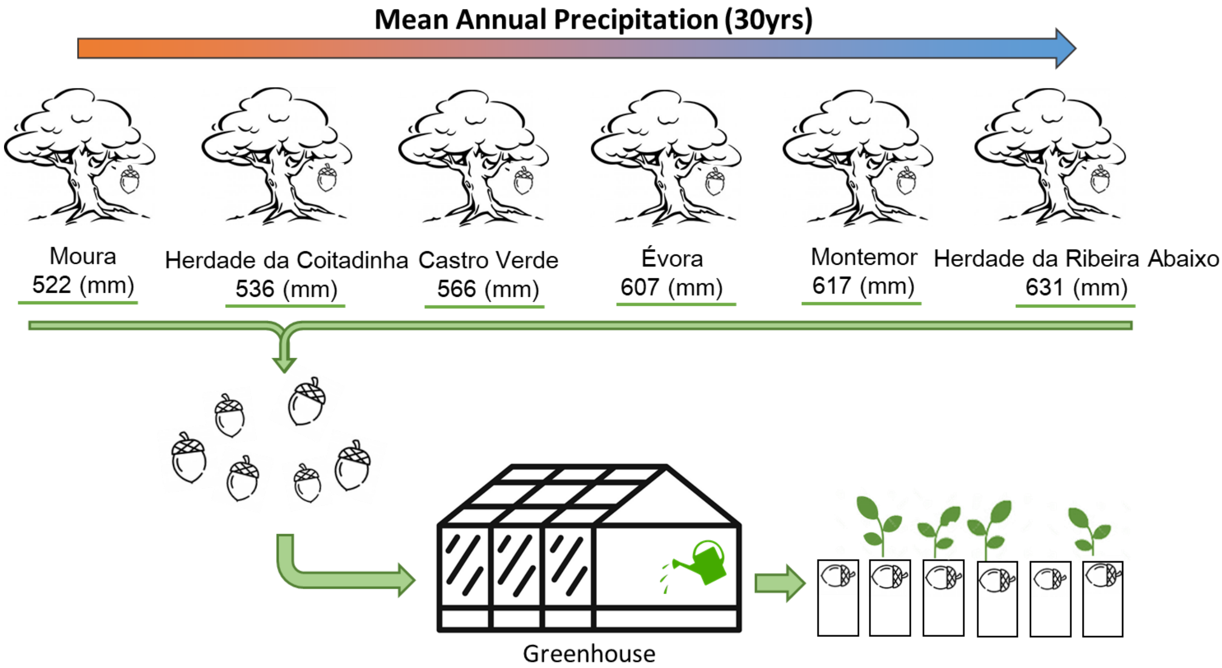

Figure 4. Schematic representation of a) acorn sampling sites across a gradient of precipitation; b) germination under similar conditions in a greenhouse in Faculty of Sciences, University of Lisbon; c) data collecting, germination count.

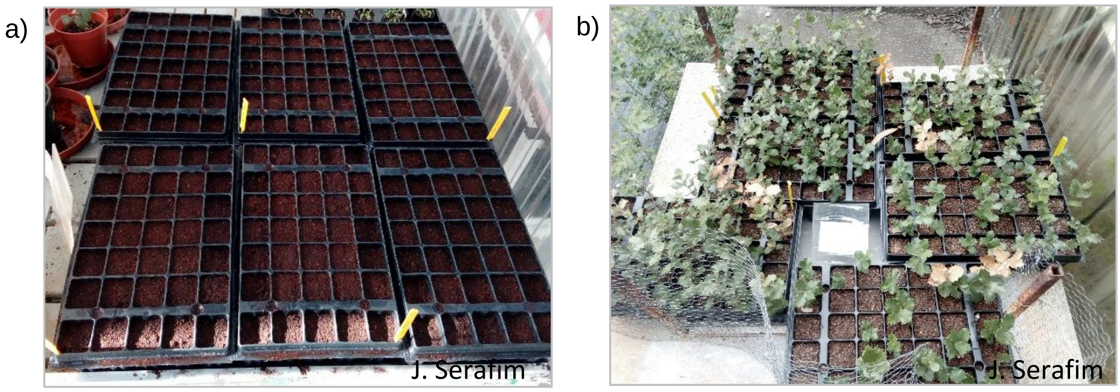

Figure 5. Acorn sowing under similar conditions. a) Germination were kept inside the greenhouse; b) later on the trays with the germinated seedlings were placed outside of the greenhouse.

2.2.2 – Testing the effect of microclimate in the drier and the wetter site

To study the influence of microclimate on Holm oak germination and establishment, alone and in interaction with macroclimatic provenance (from the six sites) and growing conditions (in a drier and a wetter site), another experimental set was placed in the two LTER sites mentioned previously, namely in Herdade da Coitadinha - called hereafter “drier site”, (Fig. 6.i), and in Herdade da Ribeira Abaixo – called hereafter “wetter site” (Fig. 6.ii).

In each of these two sites, two areas with contrasting microclimatic conditions**,** i.e. areas more exposed to the sun radiation (roughly speaking, south facing slopes) and less exposed (north facing slopes) were selected, using Potential Solar Radiation (PSR). PSR represents the amount of energy provided by radiation received in a certain point, considering the surrounding topography, altitude, latitude and longitude, as well as the direct and reflected radiation. Radiation covered by clouds is not considered; however, at a local scale clouds will affect similarly PSR calculations for both more exposed and less exposed areas. Using maps of PSR generated by ArcGIS software, areas more exposed (high PSR) and less exposed (low PSR) were selected in Herdade da Coitadinha (drier site) and Herdade da Ribeira Abaixo (wetter site) (Fig. S1; Fig. S2). These PSR maps were obtained from digital terrain model, with a resolution of 10m x 10m. Afterwards microclimatic contrasting conditions were further confirmed in the field through the use of sensors to measure air temperature and relative humidity (Fig. S3; Fig. S4)

- Acorn microclimate provenance

To test the effect of microclimate provenance on Holm oak, acorns were collected (as explained in section 2.2.3.) in areas with contrasting microclimate conditions (high and low PSR) within each of the two LTER sites. In Herdade da Ribeira Abaixo only 3 trees were sampled in low PSR areas (north-facing slope) and 2 in high PSR areas (south-facing slope) due to a lack of Holm oak trees, while in Herdade da Coitadinha 5 trees where sampled for each microclimate. Acorns from different microclimatic provenances were stored and characterized as described in section 2.2.3 and were set to germinate under similar conditions in the greenhouse (see section 2.2.1).

- Germination and survival in trays under field conditions

The acorns collected in autumn 2017 were set to germinate under field conditions in germination trays (6x6x16cm), placed in low and high PSR areas in the drier and the wetter sites. Germination in trays with commercial soil (Substrato especial Germinação, SIRO) was done to avoid the effect of confounding factors derived from potential differences in soil between sites and microclimate areas. Half of the acorns were set to germinate in the original slope (high or low PSR class, Fig. 6b, Fig. 6d) and the other half in the opposite one (Fig. 6a, Fig. 6c), making a reciprocal seed exchange, within each LTER site. In total 51 acorns from each provenance in each microclimate were put to germinate in the field, divided in three replica trays of 17 acorns per provenance (Fig. 7a-b). Germination was considered once the seedling emerged from the soil.

To avoid acorn predation the trays were protected using a wire mesh. In each of the trays a sensor (iButton hygrocrom) measuring air temperature and relative air humidity was placed to assess the microclimate driven by topography *in loco*. Data was collected using the software OneWireViewer.

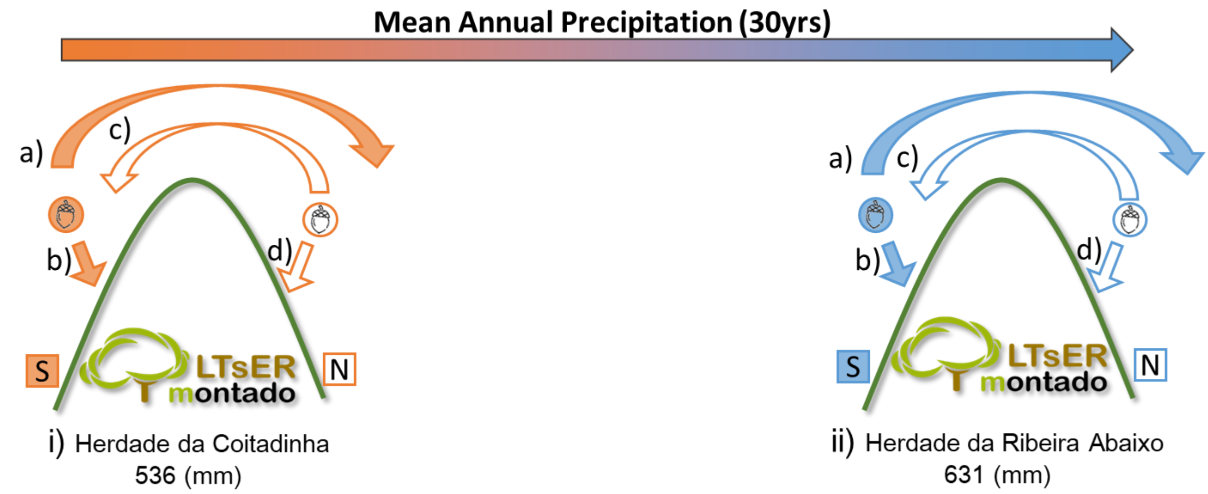

Figure 6. Schematic representation of acorns sown under contrasting microclimate conditions, in both the drier i) and wetter site ii); a) acorns with south provenance (S = high PSR) set to germinate in a northern slope (N = low PSR); b) acorns with south provenance (S = high PSR) set to germinate in a southern slope (S = high PSR); c) acorns with northern provenance (N = low PSR) set to germinate in a southern slope (S = high PSR); d) acorns with northern provenance (N = low PSR) set to germinate in a northern slope (N = low PSR).

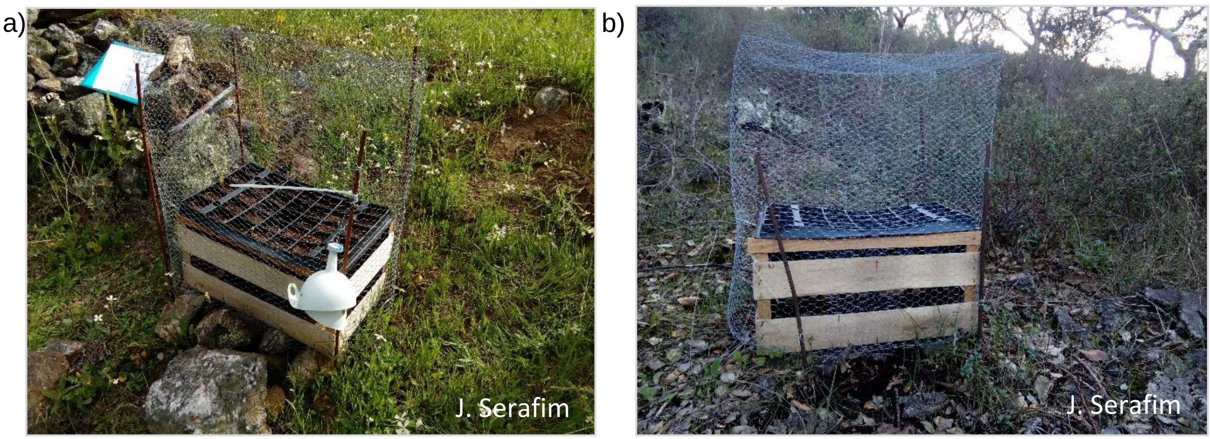

Figure 7. Germination trays with wire mesh copulated in the field. Each picture shows one of the six structures were acorns were set to germinate in each extreme of the mean annual precipitation gradient: a) drier site; b) wetter site.

- First summer drought survival of transplanted seedlings, in soil under field conditions

In autumn 2018, one-year old seedlings with different macroclimatic provenances (obtained from 2.2.1; Fig. 8a-c) were transplanted directly to the soil in the drier and wetter sites, under contrasting microclimatic conditions, i.e. slopes with high and low PSR (Fig. 8d). The seedlings were divided by four different conditions (high and low PSR, each within the drier and wetter sites; Table 3; Fig. 8a-c). The planting area for the seedlings in each site was selected using the PSR maps (Fig. S1; Fig. S2). Seedlings were transplanted to a manually opened hole with ca. 20 cm depth. Seedlings with different provenances were placed mixed randomly within each area (Fig. 9a). To each seedling a 60 cm plastic protection tube was added to protect the seedling from herbivory (Fig. 9b). Seedling survival was monitored until the first summer after transplant.

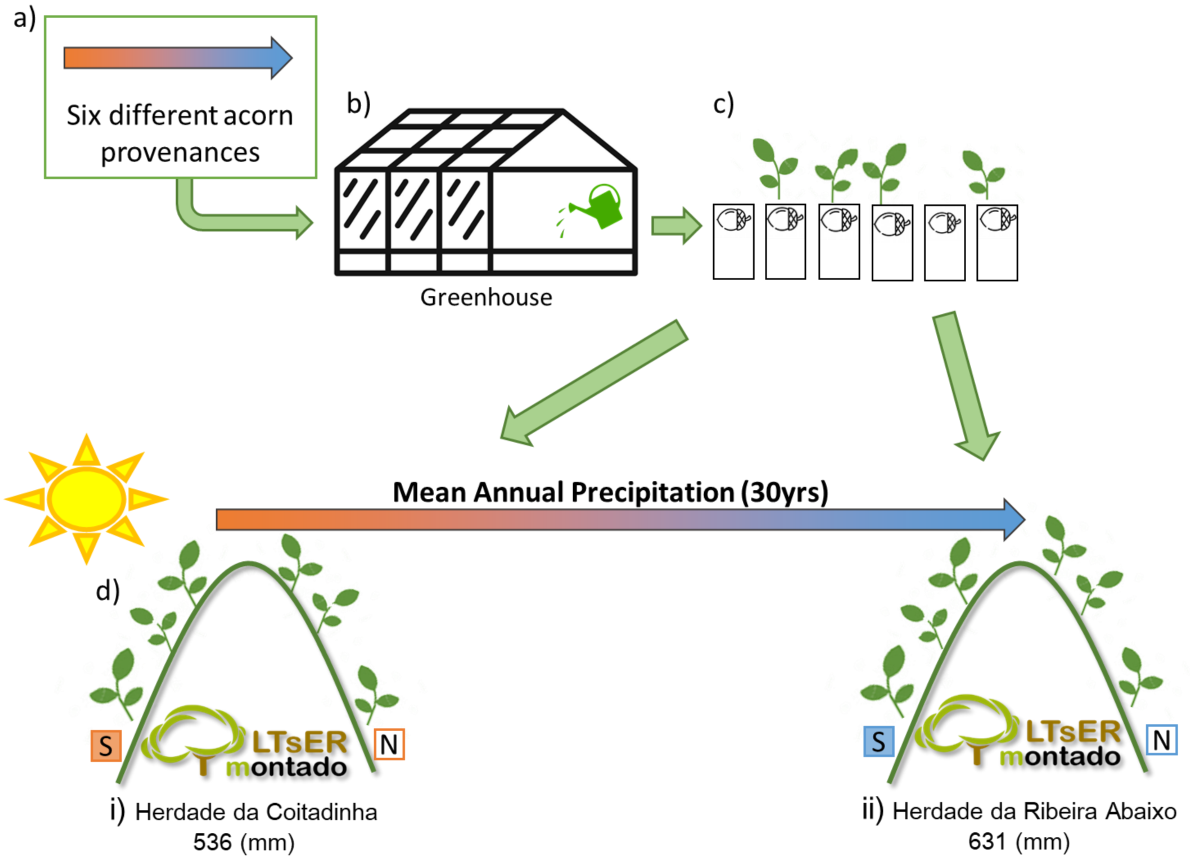

Figure 8. Schematic representation of seedling transplant to different field conditions: a) acorns collected from different macroclimate provenances; b) acorn germination under similar conditions; c) seedlings with different provenances; d) seedling transplant to contrasting conditions, southern (S) and northern (N) slopes, in both the drier i) and wetter ii) sites.

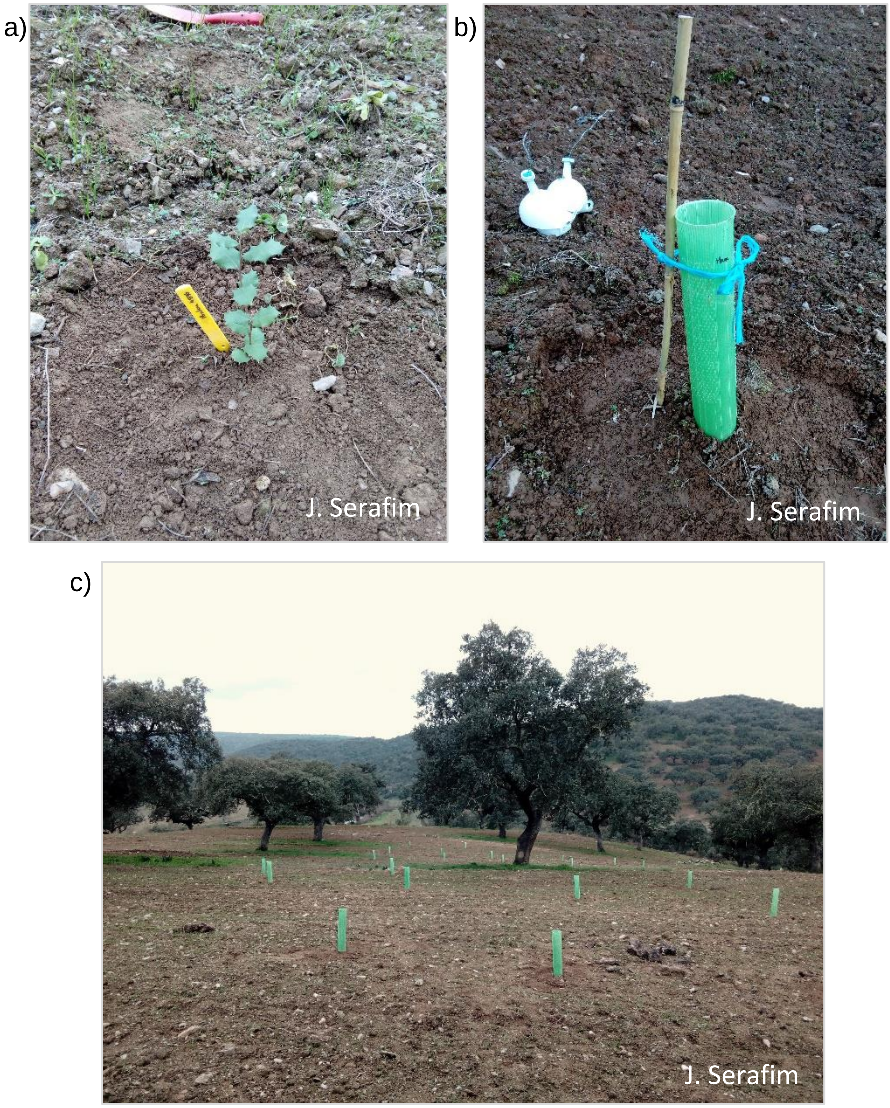

Figure 9. Field seedling transplant: a) soil seedling transplant before assembling the protective plastic tube; b) seedling transplant with the protective plastic tube assembled; c) transplantation plot in the dry site.

Table 3. Summary of the number of seedlings from different provenances grown in the greenhouse and transplanted afterwards to contrasting field conditions ($N \geq 3$). The number of transplanted seedlings varies according to the number of acorns that germinated and survived under greenhouse conditions in each case.

MAP	Macroclimatic provenance	Drier Site		Wetter Site	
		High PSR	Low PSR	High PSR	Low PSR
522	Moura	6	6	6	6
536	Herdade da Coitadinha	6	6	6	7
566	Castro Verde	6	6	8	5
607	Évora	7	6	6	7
617	Montemor-o-Novo	4	3	5	4
631	Herdade da Ribeira Abaixo	3	4	4	3
	Total	32	31	35	32

2.2.3 – Acorn sampling and characterization, and acorn production

In the first sampling year (2017), acorns were collected from at least 5 trees in each site and mixed in a composed sample. Ripped, apparently healthy, whole acorns without holes were collected from the ground.

In the second sampling year (2018), acorns were sampled from 5 trees in each site similarly to the previous sampling. Acorn production *per* m^2 was evaluated for each tree by quantifying the number of acorns fallen on the ground within 4 squares of 0.25 m^2 placed under the canopy, 2 m away from tree trunk, uniformly in cardinal orientation (Fig. 10). For each sampled tree, trunk diameter at 1.35 m height and two perpendicular diameters of the canopy (*A* and *B)* were measured. Canopy area was calculated using the approximation of an ellipsoid (Equation 1). Tree height was measured using a Hypsometer (Nikon, Forestry Pro Hypsometer).

Acorns were put in a paper bag and taken to the lab. In 2017 (dry year) acorns were placed in a mesh above water not to desiccate, at room temperature. For each of the six samples, 35 acorns were set to germinate under greenhouse conditions, and the fresh weight of the remaining ones was measured afterwards. In 2018 (normal year) acorns were brought to the lab, measured immediately after, and stored in a refrigerator at 4°C for two weeks. After that they were set to germinate in the greenhouse.

In both years, to characterize the acorns from each site, 15 acorns from each composite sample were individually weighted and their length and diameter measured using a digital caliper (Mitutoyo, Digimatic Caliper). Volume was calculated using an approximation of an ellipsoid (Equation 2). Acorn specific weight was calculated dividing the weight by the volume (Equation 3). In the greenhouse germination experiment of 2018, besides a characterization of acorns form the composite sample, each sown acorn was individually characterized prior to sowing (N=25).

Equation 1 –Tree canopy area, approximation to an ellipsoid.

$$Canopy\ area = \pi \times \left(\frac{Diameter\ A}{2}\right) \times \left(\frac{Diameter\ B}{2}\right)$$

Equation 2 – Acorn volume, approximation to an ellipsoid.

$$Acorn\ volume = \frac{3}{4} \times Lengh \times \left(\frac{Diameter}{2}\right)^2$$

Equation 3 – Acorn specific weight.

$$Acorn\ specific\ weight\ = \frac{Acorn\ Weight}{Acorn\ Volume}$$

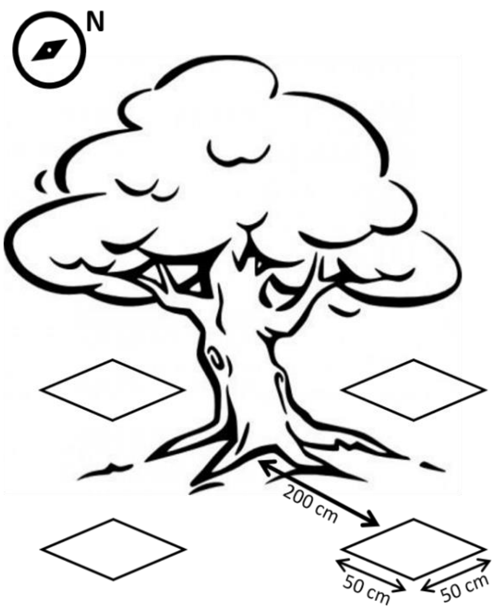

Figure 10. Schematic representation of acorn production quantification, each square at 2 m from the tree trunk represents the projection of 0.25m^2 of canopy.

2.2.4 – Soil analyses

Topsoil samples were collected from the drier and wetter sites, and also from the two areas with contrasting microclimate conditions in each site, to which Holm oak seedlings were transplanted, to help results' interpretation. In each case, one composite sample was collected, consisting of 5 cores of 500g of soil from 0 cm – 10 cm depth, mixed afterwards. Prior to soil analysis, samples were dried at 60°C in an oven and sieved using a 2 mm sieve. The following soil analyses were then made for each sample:

- Soil organic matter (SOM) and soil carbonates (SC) content were calculated by weight loss in ignition at 600° C and 900° C (Heiri et al. 2001), respectively, in a Muffle furnace (Nabertherm, Muffle furnace L3 11/16). Prior to incineration soil samples were left to dry out for 48h at 60°C and soil weight registered. Soils burned in the furnace for 6h, and afterwards they were cooled in the furnace for 4h. The samples were transferred to a hermetic box with a desiccant, to prevent them to absorb air humidity. After complete cooling the weight after ignition was measured. SOM and SC were calculated using the proportion burnt in the furnace (Equation 4; Equation 5).

Equation 4 – Soil organic matter content, loss in incineration (%).

$$SOM(\%) = \frac{Soil\ weight\ (60°C) - Soil\ weight\ after\ ignition\ (600°C)}{Soil\ weight\ (60°\ C)} \times 100$$

Equation 5 – Soil carbonate content, loss in incineration (%).

$$SC(\%) = \frac{Soil\ weight\ (60°C) - Soil\ weight\ after\ ignition\ (900°C)}{Soil\ weight\ (60°\ C)} \times 100$$

- To measure soil pH, 3 readings per sample were done with the Direct soil pH Measurement Kit from Hannah Instruments.

- To quantify soil granulometry, an automatic vibratory sieve shaker (Fritsch Analysette 3, Fritsch, Idar-Oberstein, Germany) was used with 3 sieve sizes: 2 mm, 425 μm and 63 μm. Resulting fractions were weighed separately and coarse sand (> 2000 μm), medium sand (2000 μm - 425 μm), fine sand (425 μm - 63 μm) and silt & clay fraction (< 63 μm) determined (Jahn et al. 2006). The proportion of each fraction was calculated relative to the initial amount of soil introduced (about 100 g per sample) in the vibratory sieve shaker.

2.3 – Data analysis

Firstly, along with a graphical exploratory analysis of the data obtained, the significance of the correlations between all predictor and response variables was tested using Spearman correlation, to account for possible non-linear relationships. Secondly, general linear models were built to test the effect of macroclimate, microclimate, and their interaction (predictors) on Holm oak performance (response variables) under controlled (greenhouse) and field conditions, namely on: 1) germination, 2) survival, 4) tree dimensions, 5) acorn production (number of acorn/m^2) and 6) soil characteristics. Mean annual precipitation (MAP) of the different sites was used as a proxy of macroclimate, while potential solar radiation (PSR) was used as a measure of microclimate. In some models, the significance of a quadratic term for MAP or PSR was also tested, to account for non-linear (unimodal) relationships. Generalized linear models were also used to test the effect of predictors on germination, using Binomial distributions (binary data). Statistical analysis was done with R software (R Core Team, 2016).

3 – Results

3.1 – Effect of Macroclimate

3.1.1 – Provenance on acorn weight

The biometric measurements used to characterize acorns (length, width, weight, volume and specific weight) from different macroclimate provenances were highly correlated with each other (Table S2). Therefore, acorn weight was selected to represent acorn size. For the dry year (2017), acorns fresh weight decreased with mean annual precipitation (Fig. 11).

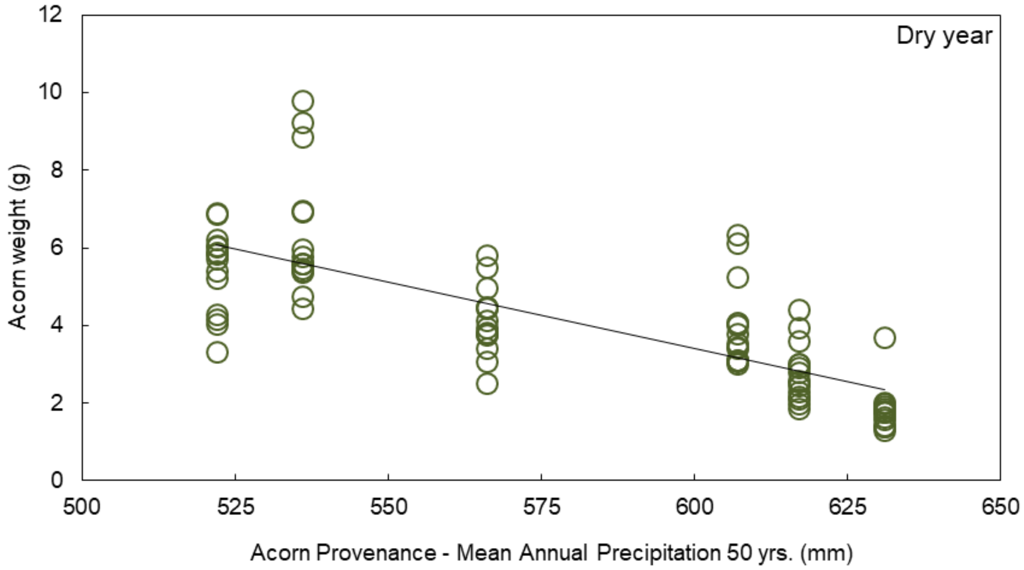

Figure 11. Weight variation of acorns collected along the macroclimate gradient (different macroclimate provenance), based on mean annual precipitation; acorn composite samples (N = 15) from 6 sites, collected in the fall of 2017 (dry year). The line represents the linear fit of the model (p-value < $2.2e^{-16}$; R^2 = 0.58) (Table S1).

The fresh weight of acorns collected in the normal year (2018) followed a similar trend, decreasing with mean annual precipitation (50 yrs.) (Fig. 12).

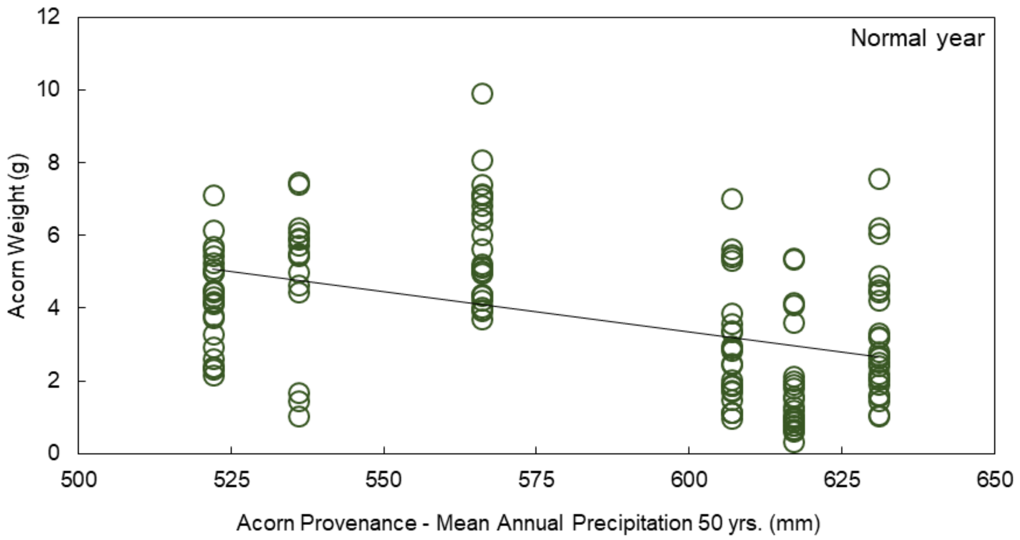

Figure 12. Weight variation of acorns collected along the macroclimate gradient (different macroclimate provenance), based on mean annual precipitation; acorn composite samples (N = 25) from 6 sites,

collected in the fall of 2018. The line represents the linear fit of the model (p-value = $2.93e^{-08}$; $R^2 = 0.19$) (Table S1).

Yet, the weight of the 15 biggest acorns collected in the normal year; showed the opposite trend, i.e. it increased with mean annual precipitation (50 yrs) (Fig. S5; Table S1).

3.1.2 – Provenance on acorn production

No significant correlation was found between acorn production (number of acorns per m^2) and mean annual precipitation of the corresponding sites, nor with Holm oak tree dimension (Table S4). Yet, acorn weight showed a marginal negative correlation with acorn production, although weak (Fig. 13, Table S4).

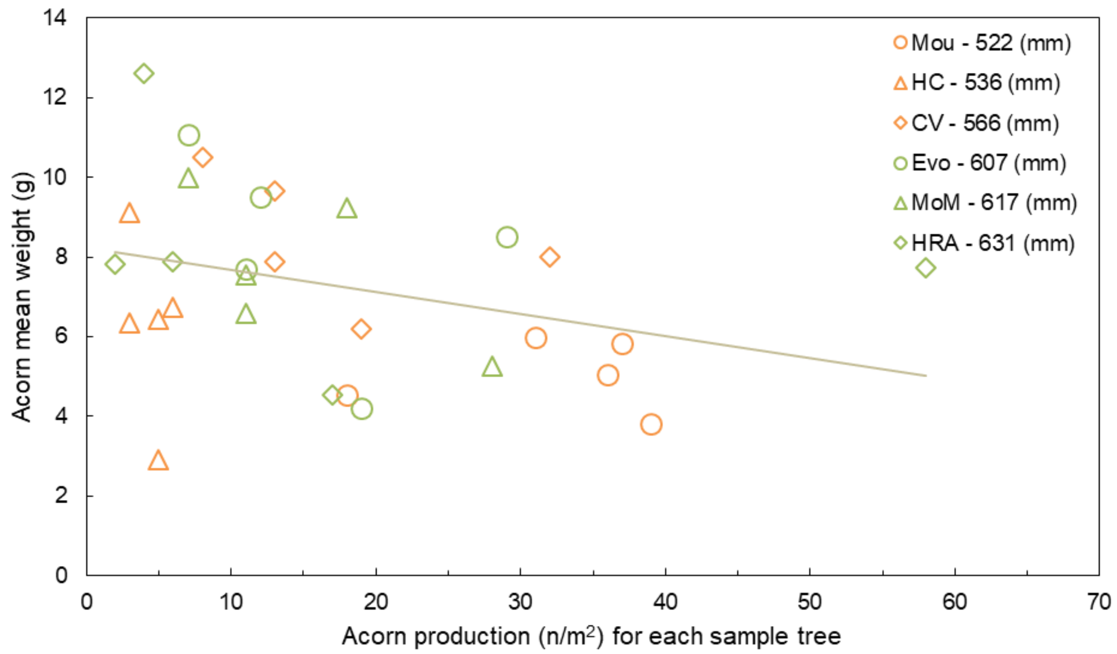

Figure 13. – Acorn mean weight per tree (N = 15) in relation to acorn production of the same tree in the six sites distributed along the macroclimate gradient. N = 5 trees per site; the line represents the linear fit to the model (p-value = 0.053; $R^2 = 0.06$).

3.1.3 – Provenance on germination in trays in the greenhouse

The germination of acorns collected from different macroclimate provenances in the dry year and sown under similar conditions in the greenhouse, showed a unimodal relation with mean annual precipitation (50 yrs.). Acorn germination was lower for acorns collected in the drier and wetter extremes of the climatic gradient, and higher for acorns from intermediate sites (Fig. 14).

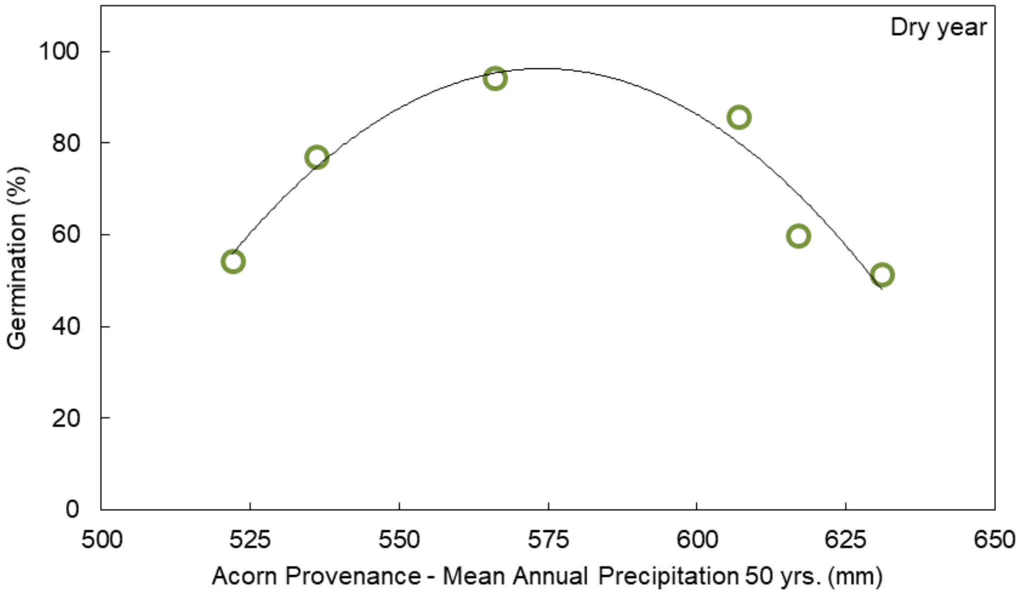

Figure 14. Germination percentage of acorns collected along the macroclimate gradient (different macroclimate provenance), based on mean annual precipitation; acorn composite samples (N = 35) from 6 sites, collected in the fall of 2017. The line represents the overall trend, observed in the quadratic fit of the generalized linear model (p-value = $3.41e^{-6}$; pseudo-R^2 = 0.10) (Table S1).

Contrastingly, the germination of acorns collected in the normal year and set to germinate under greenhouse conditions, decreased linearly with provenance mean annual precipitation. Acorns collected at the wetter extreme of the climatic gradient showed lower germination percentage than those from the drier extreme (Fig. 15; Table S1). In addition, acorns collected in the normal year showed in general lower germination percentage (under 50%) than those collected in the dry year (above 50%), for all provenances.

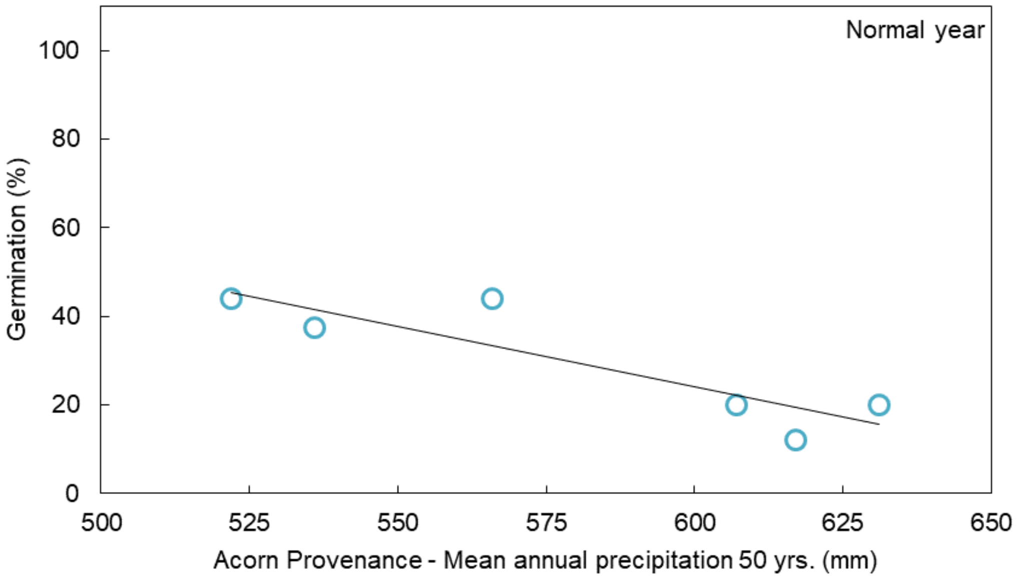

Figure 15. Germination percentage of acorns collected along the macroclimate gradient (different macroclimate provenance), based on mean annual precipitation; acorn composite samples (N = 25) from 6 sites, collected in the fall of 2018. The line represents the overall trend, observed in the fit of the generalized linear model (p-value = 0.003; R^2 = 0.05; Table S1).

The specific weight of acorns that germinated was in general higher than of the acorns that did not germinate (Fig. 16; Table S1). Acorn specific weight showed a decreasing trend with provenance mean annual precipitation (Fig. 16; Table S1), as well as germination percentage (Fig. 15; Fig. 16;Table S1; Table S4).

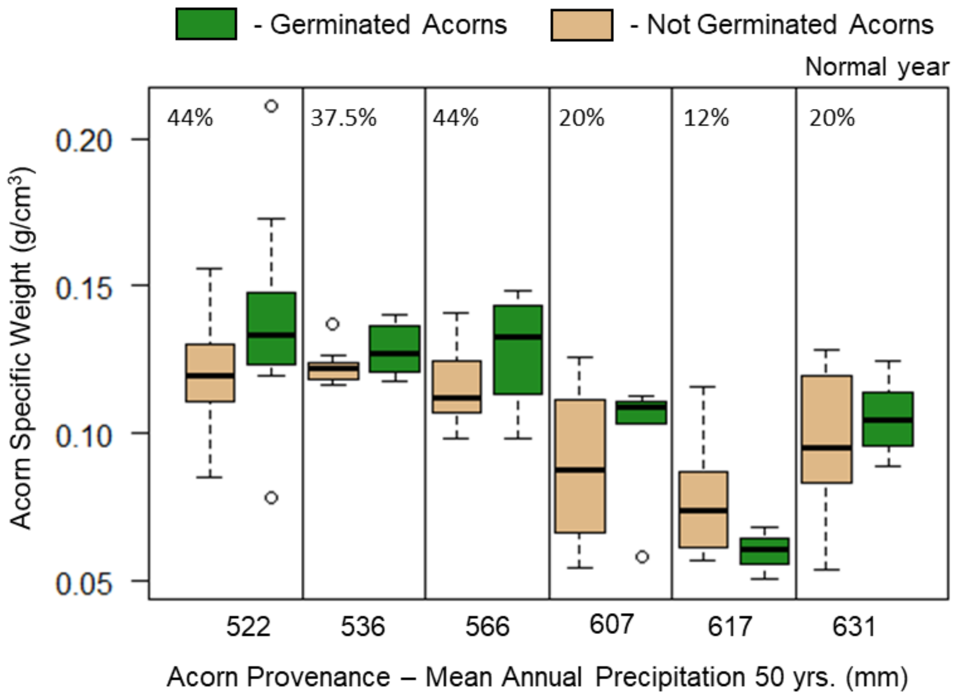

Figure 16. Acorn specific weight (g/cm^3) distribution along the macroclimate gradient (different macroclimate provenance) for germinated acorns (green) and non-germinated acorns (brown), (N = 25) Acorn specific weight was higher for acorns that geminated (p-value = 0.0003; R^2 = 0.09) and decreased with provenance mean annual precipitation (p-value = 1.009 e^{-15}; R^2 = 0.38). Germination percentage decreased with provenance mean annual precipitation (p-value = 0.003; R^2 = 0.05).

3.1.4 – Provenance on young seedling survival in the greenhouse

Seedlings with different mean annual precipitation (50 yrs.) provenance form acorns collected in the dry year show a high survival (80%-100%) in similar conditions (Fig.17). The relation with provenance was not significant (p-value = 0.45; Table S1).

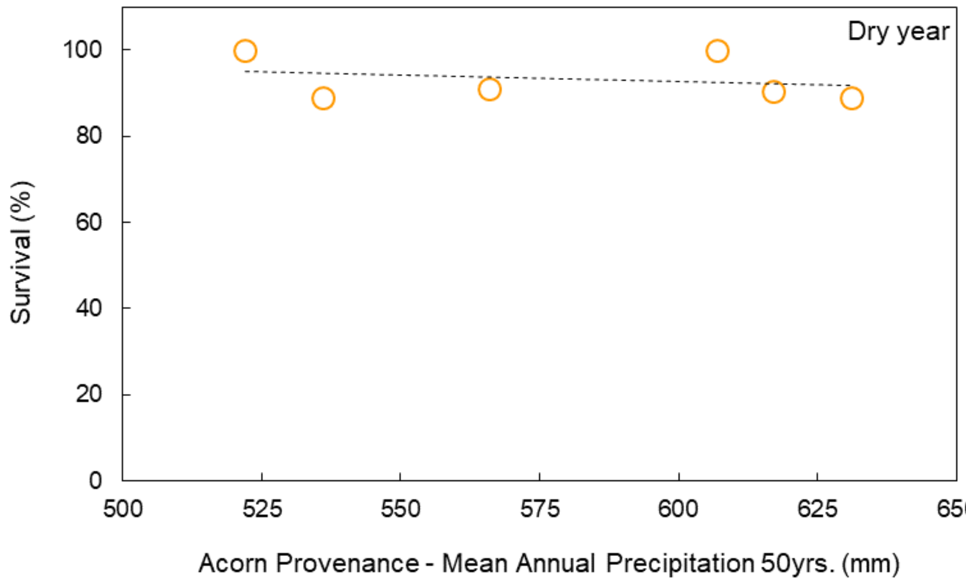

Figure 17. One-year old seedling survival percentage, originating from acorns collected along the macroclimate gradient (different macroclimate provenance), based on mean annual precipitation; from 6 sites, collected in dry year (N ≥ 18). The line represents the overall trend, observed in the fit of the generalized linear model (p-value = 0.45; R^2 = 0.06) (Table S1).

For the normal year, the percentage of survival showed a tendency to increase with mean annual precipitaion (50 yrs.) provenance, however it was not significantive.

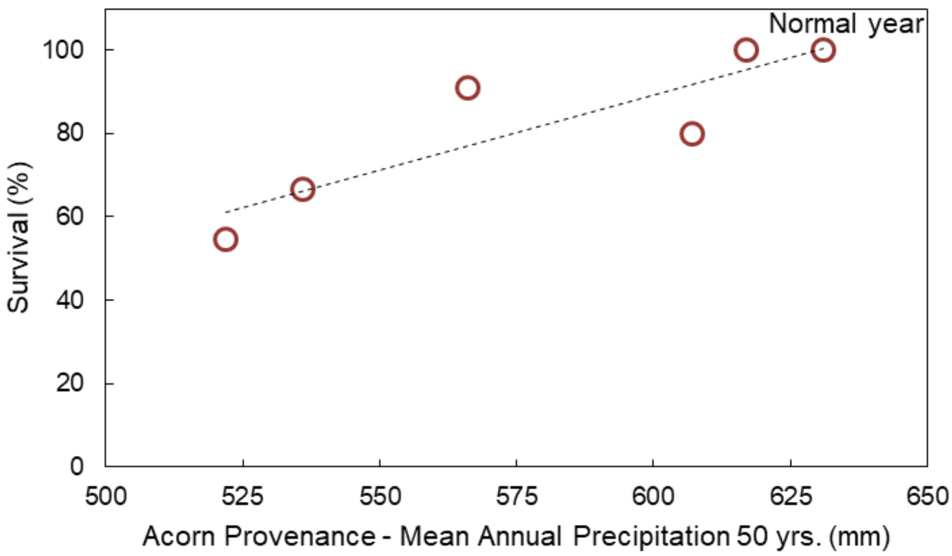

Figure 18. One-year old seedlings survival percentage, originating from acorns collected along the macroclimate gradient (different macroclimate provenance), based on mean annual precipitation; from 6 sites, collected in the normal year (N ≥ 3). The line represents the overall trend, observed in the fit of the generalized linear model (p-value = 0.997; R2 = 0.39) (Table S1)

3.2 – Effect of microclimate and macroclimate

3.2.1 – Provenances on acorn weight

The weight of acorns collected in the dry year in more exposed areas (High PSR) was higher than of those collected in areas with low exposition (Low PSR) (Fig. 19). In general, acorn weight was higher for acorns collected in the drier site (orange) than of those from the wetter site (blue) (Fig. 19).

The significant negative interaction between microclimatic (PSR) provenance and macroclimate (MAP) provenance in explaining acorn weight (Table 4) indicates that the effect of microclimate provenance on acorn weight is stronger for acorns collected in the drier site (lower mean annual precipitation) than for those from the wetter site (Fig. 19; Table 4).

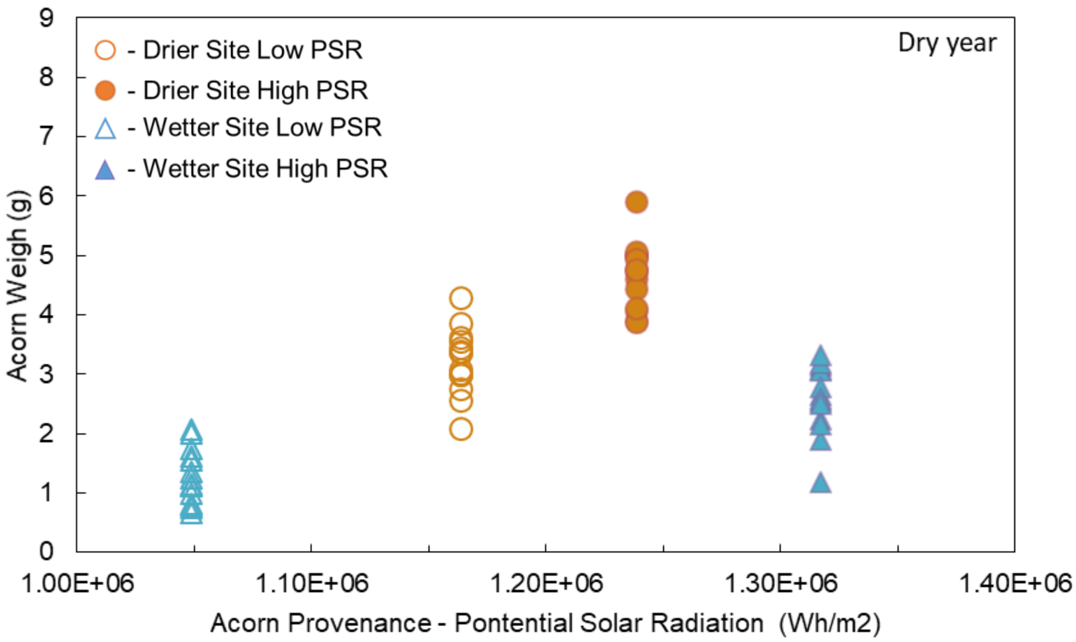

Figure 19. Weight variation of acorns collected in different microclimates; acorn composite samples (N = 15) from 2 microclimates x 2 sites, collected in the fall of the dry year (2017). The effect of microclimate and macroclimate provenances and of their interaction was tested with a linear model (see Table 4 for model summary). Orange circles represent acorns collected in the drier site and blue triangles represent acorns collected in the wetter site. Full characters represent acorns collected in the high PSR area and empty characters represent acorns collected in the low PSR area.

Table 4. Linear model summary to test the effect of microclimate and macroclimate provenances, and of their interaction, on acorn weight in the dry year (2017): AW- Acorn weight; PSRp – Potential Solar Radiation of acorn provenance; MAPp – Mean Annual Precipitation (50 yrs.) of acorn provenance.

Response variable	Predictor	Estimate	p-value	R^2
AW	PSRp	0.709	1.36 e^{-09}	0.66
	MAPp	-0.555	6.87 e^{-08}	
	PSRp*MAPp	-0.276	0.0199	

In the normal year, acorn weight showed a trend similar to the dry year, i.e. it was higher for acorns collected in more exposed areas (High PSR) than for those collected in areas with low exposition (Low PSR), and was higher for the drier site provenance than for the wetter site provenance (Fig. 20; Table 5). However, for the normal sampling year the interaction between microclimate (PSR) and macroclimate (MAP) was not significant (Table 5).

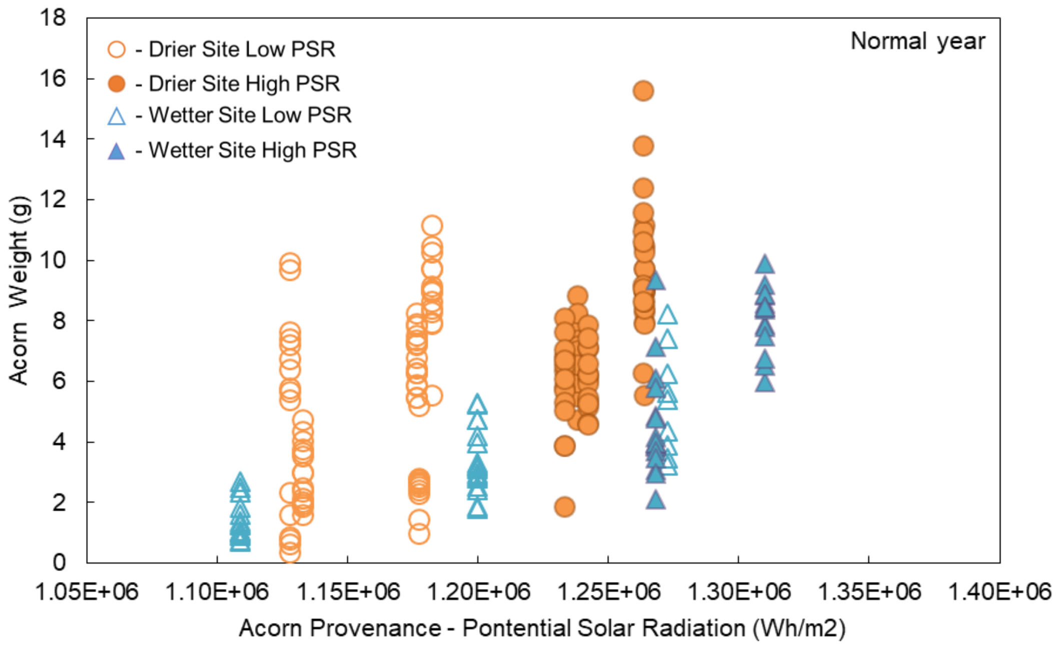

Figure 20. Weight variation of acorns collected in different microclimates; acorn composite samples (N = 15) from 2 microclimates x 2 sites, collected in the fall of normal year (2018). Orange circles represent acorns collected in the drier site and blue triangles represent acorns collected in the wetter site. Full characters represent acorns collected in the high PSR area and empty characters represent acorns collected in the low PSR area.

Table 5. Linear model summary to test the effect of microclimate and macroclimate provenances on acorn weight in the normal year (2018). AW – Acorn weight; PSRp – Potential solar radiation of acorn provenance; MAPp – Mean Annual precipitation (50 yrs.) of acorn provenance; ns – no significance.

Response variable	Predictor	Estimate	p-value	R^2
AW	PSRp	0.609	<2.00 e^{-16}	0.44
	MAPp	-0.447	3.04 e^{-15}	
	PSRp*MAPp	-0.020	ns	

3.2.2 – On germination in trays in the field

Acorns collected in the dry year with provenance from more exposed areas (high PSR; full symbols) had higher germination than those coming from less exposed areas (low PSR; open symbols) at each site (Fig. 21; Table 6). Acorns from the drier site placed in trays *in situ* (orange symbols) had a higher germination than those in the wetter site (blue symbols) (Fig. 21; Table 6). However, regarding the microclimatic conditions in the field where the germinations trays were placed, no consistent differences were found in germination between acorns placed in high and low PSR conditions, as shown along the x axis (Fig. 21; Table 6). Hence, germination was better explained by PSR of provenance (PSRp) and Mean Annual Precipitation (MAP) (Table 6).

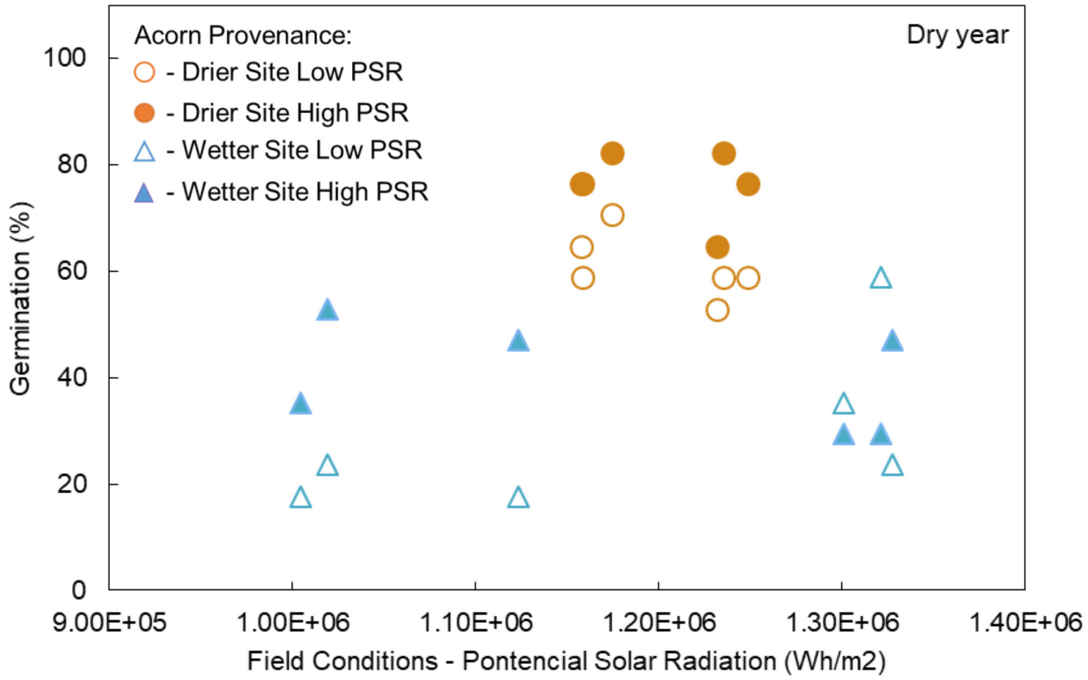

Figure 21. Germination percentage across different microclimatic (PSR) conditions of acorns collected from different provenances. Orange circles represent acorns collected in the drier site and blue triangles represent acorns collected in the wetter site. Full characters represent acorns collected in the high PSR area and empty characters represent acorns collected in the low PSR area; acorn composed sample (N = 51). The effect of microclimate and macroclimate and of their interaction was tested with a general linear model (see Table 6 for model summary).

Table 6. Generalised linear model (binomial) summary that shows the effect of microclimate and macroclimate provenances, and their interaction, on acorn germination. AFG – Acorn field germination; PSRd – Potential solar radiation to each the acorns were sown; PSRp – Potential solar radiation of acorn provenance; MAPp – Mean Annual precipitation (50 yrs.) of acorn provenance; ns – no significance.

Response variable	Predictor	Estimate	p-value	Pseudo- R^2
AFG	PSRp	0.596	0.00391	0.10
	PSRd	-	ns	
	MAP	-0.778	5.42 e^{-10}	
	PSRp*MAP	-0.413	ns	
	PSRd*MAP	-	ns	
	PSRp*PSRd	-	ns	
	PSRp*PSRd*MAP	-	ns	

3.2.3 – On germination in trays in the greenhouse

Under similar greenhouse conditions, acorns collected in the normal year from more exposed areas (High PSR; full symbols) had higher germination than those from less exposed areas (Low PSR; open symbols), for both the drier and the wetter sites (Fig. 22; Table 7). Also, acorns collected in the drier site (orange symbols) had higher germination than those from the wetter site (blue symbols) (Fig. 22; Table 7), following the same pattern found under field conditions (Fig. 21).

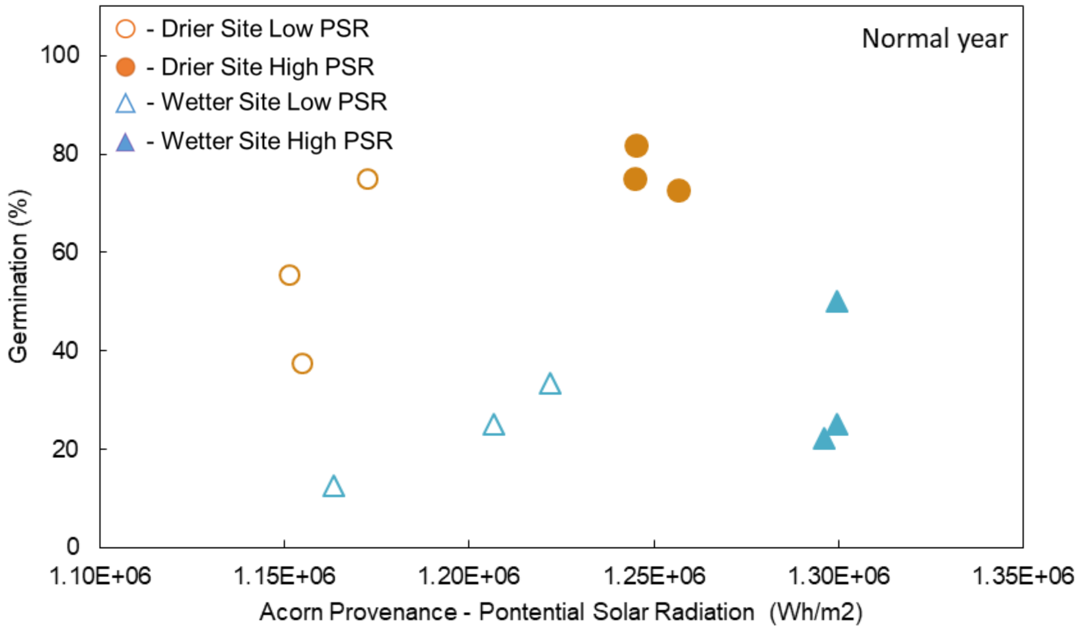

Figure 22. Germination percentage of acorns collected from different provenances, high and low PSR on the drier site and wetter site, in trays under similar greenhouse conditions; acorn composed sample (N = 25). The effect of microclimate and macroclimate provenances and of their interaction was tested with a generalized linear model (see Table 7 for model summary).

Table 7. Generalized linear model (binomial) summary that shows the effect of microclimate and macroclimate provenances on acorn germination under similar conditions in the green house (2018/2019). AG – Acorn germination; PSRp – Potential solar radiation of acorn provenance; MAPp – Mean Annual precipitation (50 yrs.) of acorn provenance; ns – no significance.

Response variable	Predictor	Estimate	p-value	R^2
AG	PSRp	0.515	2.33 e-05	0.14
	MAPp	-1.052	0.038	
	PSRp*MAPp	-0.027	ns	

3.2.4 – On young seedling survival in trays in the field

Seedling survival until mid-summer of 2018 of seedlings from acorns collected and sown in autumn 2017 (dry year) and placed in trays *in situ* was higher in less exposed areas (Low PSR field conditions) than in more exposed areas (High PSR field condition), as shown along the x axis, despite their microclimate provenance (open and full symbols) (Fig. 23; Table 8). Also, in general, seedling survival was higher in the wetter site (blue symbols) than in the drier site (orange symbols) (Fig. 23; Table 8). Thus, both microclimate and macroclimate growing conditions *in situ* influenced seedling survival, regardless of microclimate provenance (Table 8).

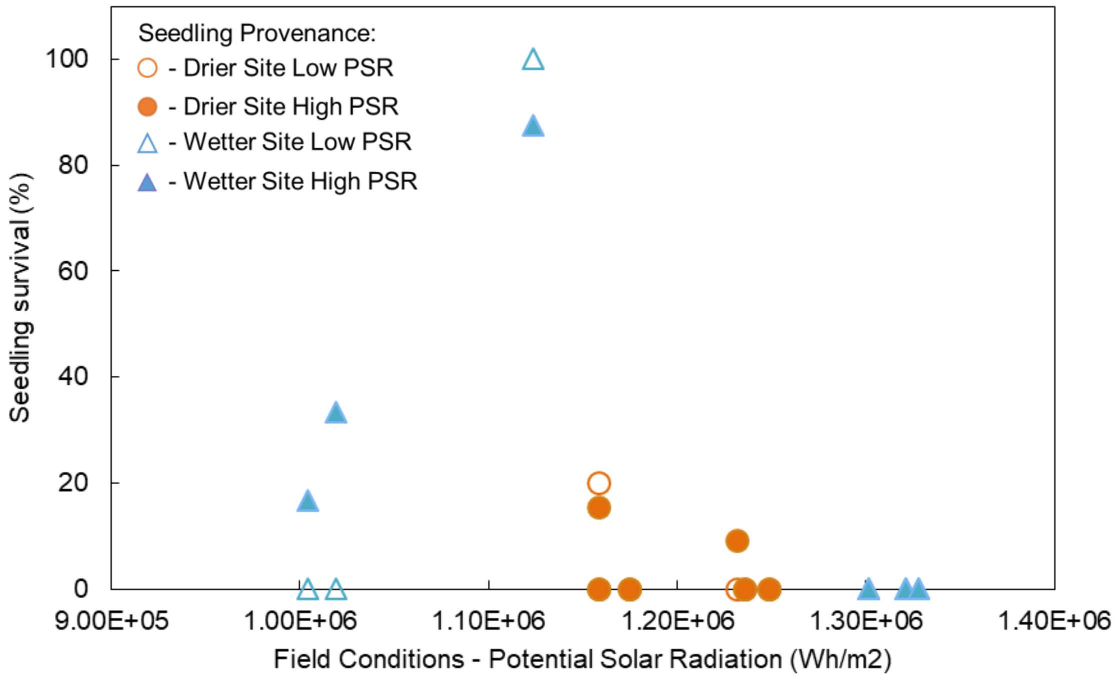

Figure 23. First year survival percentage in mid-summer 2018 of seedlings from acorns collected and sown in autumn 2017 from different microclimate provenances, namely high and low PSR (full and open symbols, respectively) placed in trays *in situ* in the drier and the wetter sites (orange and blue symbols, respectively), under different PSR conditions in the field (x axis) (N ≥ 3 seedlings from germinated acorns). The effect of microclimate and macroclimate and of their interaction on seedling survival was tested with a generalized linear model (see Table 8 for model summary).

Table 8. Generalized Linear model (Binomial) of first year survival in mid-summer 2018 of seedlings (acorns collected and sown in autumn 2017) from different microclimate provenances (high and low PSR), placed in trays across different PSR conditions *in situ* in the drier and the wetter sites. FS – Seedling field survival; PSRd – Potential solar radiation of the "destination place" where the trays with the seedlings where set; PSRp – Potential solar radiation of acorn provenance; MAP – Mean Annual precipitation (50 yrs.) of seedling provenance placed in trays *in situ*; ns – no significance.

Response variable	Predictor	Estimate	p-value	R^2
FS	PSRp	0.375	ns	0.19
	PSRd	-0.878	0.004	
	MAP	0.773	0.021	
	PSRp*MAP	-	ns	
	PSRd*MAP	-	ns	
	PSRp*PSRd	-	ns	
	PSRp*PSRd*MAP	-	ns	

3.2.5 – On young seedling survival in soil in the field

The first summer survival (July 2019) of one-year-old seedlings from different macroclimate provenances (acorns collected in autumn 2017, germinated and grown under greenhouse conditions) transplanted in Autumn 2018 to the soil in the field was higher in the less exposed areas (low PSR) compared to more exposed areas (high PSR) in both sites, and higher in the wetter site than in the drier site (Fig. 24,Fig 25; Table 9, Table 10), regardless of their macroclimate provenance (Fig. 25; Table 10; Table S3).

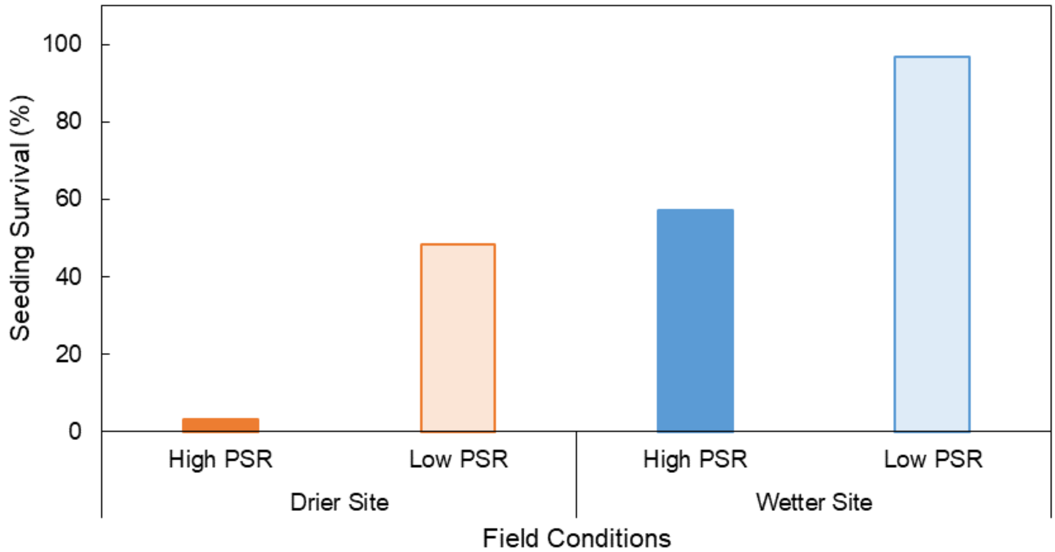

Figure 24. First summer survival in mid-summer 2019 of one-year-old seedlings transplanted to the soil in autumn 2018 under different field conditions: low and high PSR, in the drier and the wetter sites (N = 31). The effect of microclimate and macroclimate and of their interaction on seedling survival was tested with a generalized linear model (see Table 9 for model summary).

Table 9. Generalized linear model (Binomial) of first summer survival of one-year-old seedlings transplanted to the soil under different field conditions. FS – Seedling field survival; PSRd – Potential solar radiation of the "destination area" to which the seedlings where transplanted; MAPd – Mean Annual Precipitation (50 yrs.) of the site to which the seedlings were transplanted.

Response variables	Predictor	Estimate	p-value	Pseudo-R^2
FS	PSRd	-2.196	5.63 e-05	0.40
	MAPd	1.652	2.85 e-0.5	
	PSRd*MAPd	1.011	ns	

Macroclimate provenances did not influence seedling survival, but growing conditions in the field did (Fig. 25; Table 10; Table S3).

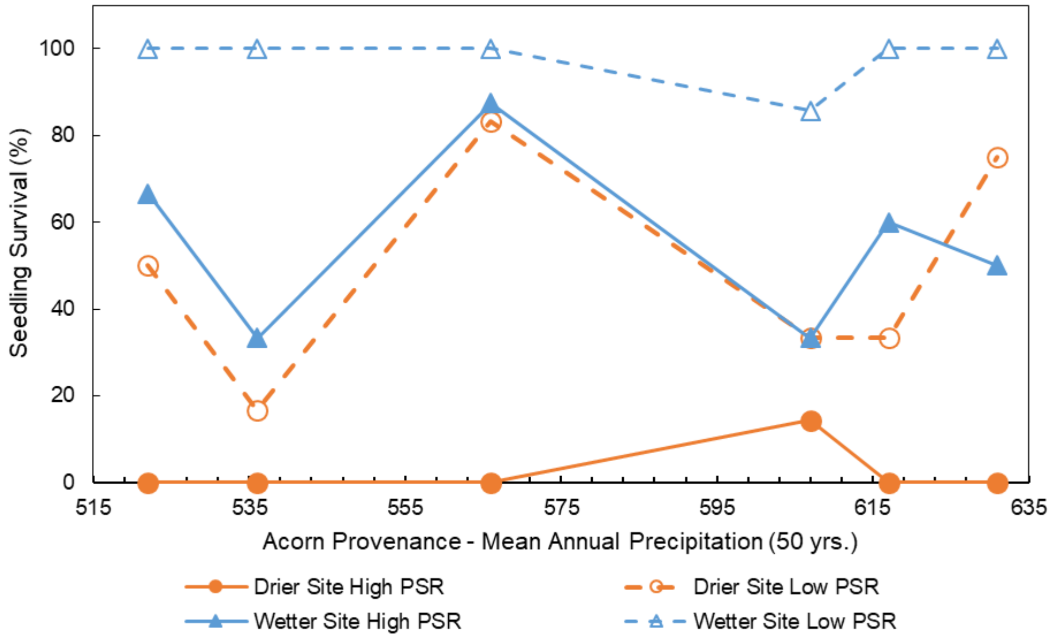

Figure 25. First summer survival in mid-summer 2019 of one-year-old seedlings from different macroclimate provenances (x axis; 6 sites with different 50 yrs mean annual precipitation) transplanted to the soil in autumn 2018 under different field conditions: low and high PSR (open and full symbols, respectively), in the drier and the wetter sites (orange and blue symbols, respectively) (N ≥ 3). The effect of microclimate and macroclimate and of their interaction on seedling survival was tested with a generalized linear model (see Table 10 for model summary).

Table 10. Generalized linear model (Binomial) of survival for transplanted seedling from 6 different provenances, under 4 different field conditions. FS – Seedling field survival; PSRd – Potential solar radiation to each the plants are transplanted; MAPd – Mean Annual Precipitation (50 yrs.) to each the plants were transplanted; MAPp – Mean Annual precipitation (50 yrs.) of plant provenance; ns – no significance.

Response variable	Predictor	Estimate	p-value	Pesudo-R^2
FS 2018	PSRd	-1.879	0.000456	0.37
	MAPp	0.013	ns	
	MAPd	1.807	1.73 e^{-05}	
	PSRd*MAPp	-	ns	
	PSRd*MAPd	-	ns	
	MAPd*MAPp	-	ns	
	PSRd*MAPp*MAPd	-	ns	

As soil characteristics (Fig. S6-S9) were highly correlated with PSR and MAP (Table S3), they were not taken under consideration as predictors to explain seedling survival in the field.

4 – Discussion

This work contributes to clarify the effect of macroclimate (at a regional scale) and microclimate (at a local scale) on Holm oak performance, namely on acorn size and germination, acorn production and on first year seedling survival. The limiting factors for Holm oak performance varied with its growing phase: acorn size and germination percentage were more influenced by their macroclimate (site mean annual precipitation) and microclimate (areas less or more exposed to solar radiation) provenances, while seedling survival after the first summer drought depended more on the macroclimate and microclimate conditions they are subjected to in the field. These findings may contribute to increase Holm oak seedling quantity and quality in nurseries and improve (re)afforestation strategies in the field. Therefore, this work provides important basis for improving the success of Holm oak (re)afforestation as a critical restoration tool to combat desertification in Portuguese drylands and revert Holm oak *Montado's* decline. In addition, it may also contribute to a better understanding of Holm oak natural regeneration patterns.

Variation in acorn size and germination with macroclimate and microclimate provenance

Acorn weight varied with macroclimate provenance, decreasing with the long-term precipitation of the site where they were collected. This trend was consistent despite inter-annual climatic variability and was observed in a dry and normal year compared to the long-term average annual precipitation. This difference was also marked between the extremes of the macroclimate gradient studied, i.e. between the drier and the wetter sites studied. A partial explanation for this, could be related with the climatic niche of Holm oak, which dominates in the drier semi-arid areas of the country (Belo et al. 2009), thus producing heavier and bigger seeds under such circumstances. In fact, the wetter site studied had a much lower number of Holm oak trees, suggesting the species is near the limit of its distribution range, compared to the drier site where it was the dominant tree. However, historically oak tree density is also a result of land users' management. that may prefer to plant Cork oak in more humid areas where it grows better and generates bigger income leaving Holm oaks to drier areas (Surová et al. 2008).

Previous works have focused on understanding acorn dimensions and its relation to production (acorn number), considering acorns are an important food source for livestock in Holm oak *Montado*s (Marañón 1988). In those studies, no clear direct correlation or trade-off was found between seed size and seed number for Holm oak, probably due to the interaction between complex factors such as seed dispersal, offspring suitability, escape from predation environmental conditions effect on phenology, among others, which do not result in valuing size over number, or *vice-versa* as a reproductive strategy of the species (Gómez 2004). Some studies have found that annual climatic variations have an effect on acorn production. Generally, at the local scale, the number of acorns produced drops in a year with lower precipitation, and in years with extreme events in the pollination and fructification period (Gea-Izquierdo et al. 2006; García-Mozo et al. 2007). Nonetheless, in this work, a weak negative trend only marginally significant was found between acorn weight and production (number of acorns) along the macroclimate gradient studied, suggesting a possible trade-off. However, to clarify the observed pattern an increase in sample size would be necessary, while keeping track of the exact same trees throughout the years.

On the other hand, at the local scale, previous works developed on specific Holm oak populations, found a higher variation in acorn weight between individuals, and size being more consistent for the same individual, throughout the years (Gea-Izquierdo et al. 2006; García-Mozo et al. 2007), suggesting acorn weight might be also linked with genetic expression. Even so, in this study, we found a consistent variation in acorn weight with microclimate provenance at the local scale, with bigger acorns collected in areas more exposed to direct solar radiation (high PSR - potential solar radiation), than in less exposed areas (low PSR). This finding was consistent for both sampling years (a dry and a normal year), and for both sites (the drier and the wetter sites) in the extremes of the macroclimate gradient studied.

Furthermore, microclimatic provenance (PSR) had a stronger effect on acorn weight, i.e. a bigger difference between acorns from high and low PSR areas, in the drier site, compared to the wetter one, and in the dry sampling year compared to the normal one. This suggest that microclimate conditions play a stronger role on acorn weight under harsher and drier conditions, showing the importance of these topography driven microclimatic ‘niches’ for Holm oak (Príncipe et al. 2014) under a future scenario of increased aridity in the Mediterranean Basin (Costa et al. 2008; Costa et al. 2012; Koutroulis 2019).

The variations found on acorn weight with macroclimate and microclimate provenance in this study are of major importance, since acorn weight showed a strong and positive correlation with its germination ability. In fact, acorn germination showed a similar trend in response to macroclimate provenance, decreasing with the long term precipitation of the provenance site, although the pattern was less clear under greenhouse conditions (where the trend was not linear for seeds collected in the dry year), than under field conditions, where germination was consistently higher for acorns collected in drier site than in the wetter site.

Germination showed a response to microclimate provenance also similar to the one of acorn weight, as acorn germination was higher for seeds collected in high PSR areas (less favorable microclimate) than in low PSR areas, in both sites. Once again, an interaction between macroclimate and microclimate was found, as the effect of microclimate provenance on germination was stronger for acorns collected in the drier site, and in the dry sampling year. Previous works describing the traditional selection of acorns to produce oak seedlings, empirically advise the selective collection of the bigger and heavier seeds, to improve success (Carecho 2015), perhaps based on empirical evidence of higher germination. Also, other authors found evidence of accelerated germination timing and increased germination rate for large acorns (Gómez 2004). These results were not in line with our initial hypothesis, as we expected a higher germination under more favourable macro- and microclimatic conditions. Even though acorns from more exposed areas are bigger and show a high potential for germination, there is previous evidence of a lower natural regeneration rate in these areas over time, when compared to less exposed areas (Príncipe et al. 2014). Possibly due to acorn recalcitrant characteristic, one would expect that harsher field microclimate conditions (besides provenance) would negatively affect acorn germination, leading to lower seedling recruitment. Interestingly, in this study, no effect of the microclimate conditions where acorns were placed in the field, was found on germination. Probably other factors like predation (Gómez 2004; Muñoz et al. 2009), dispersion (Gómez 2003), or unfavourable conditions for seedlings survival undermine Holm oak recruitment in these areas.

In addition, in general, germination in the greenhouse was higher for acorns collected in the dry year (>50%) compared to the normal year (<50%), although they had on average similar weight. This may be related to the fact that acorns collected in the normal year were kept for a longer time period in a refrigerator (4°C) before sowing, while acorns collected in the dry year were kept at room temperature and sown shortly after, considering that time and storage conditions may affect germination (Pasquini et al. 2011). Nonetheless, to fully clarify this pattern it would be necessary to specifically test the effects of these factors on Holm oak germination.

Variation in young seedling survival with macroclimate and microclimate conditions in the field

Field conditions can become a major constrain for seedling survival, as it has been described for Mediterranean species used in (re)afforestation plans, and specifically for Holm oak (Puértolas et al. 2010; Oliet et al. 2015). In this study field conditions, associated with both macro- and microclimate, were the most important factor explaining one-year old seedling survival in the first summer. For seedlings transplanted to the soil, survival was 50% higher in the wetter site than in the drier site. At a local scale, seedlings growing in less exposed areas, displaying a more favourable microclimate, with lower maximum temperatures and higher relative air humidity, showed 40% higher survival than seedlings in more exposed areas, in both extremes of the precipitation gradient. Higher survival of Holm oak seedlings growing in local favourable conditions can lead, in a long-time scale, to a considerably higher regeneration rate and cover (Príncipe et al. 2014), as well as higher (re)afforestation success in these areas when compared to more exposed areas.

By studying seedling survival growing in commercial soil in trays under contrasting macro- and microclimatic field conditions it was possible to assess their effect while avoiding the confounding effects of soil characteristics, which were different e.g. between the drier and the wetter site and highly correlated to the climatic predictors. The downside was the limited volume of the trays cells which may have constrained seedling development reducing their survival. This limitation has been overcome with seedlings transplanted directly to the soil which showed a higher survival yet responding in a similar way to macro- and microclimatic conditions.

The dramatic decrease verified in seedling survival under harsher climatic conditions (drier site and more exposed areas) calls for additional measures to ameliorate climatic constrains in the field, i.e. increase water availability (e.g. summer irrigation) and reduce temperature extremes (e.g. provide shadow). Alternatively, a good option could be to focus Holm oak sowing and planting in microclimatic favorable areas, mimicking Holm oak natural regeneration patterns reported by Príncipe and co-authors (2014). For this, we need tools that allow planning (re)afforestation efforts at a low spatial resolution, such as the ones obtained through remote sensing like PSR. These concerns are even more important under a scenario of increasing aridity in Portuguese dryland areas (Costa et al. 2008; Costa et al. 2012; Koutroulis 2019), which is expected to constrain even more Holm oak seedling survival and thus, *Montado* restoration success.

Seedling survival was explained by field growing conditions and not by climatic provenance. This is in line with previous study showing that Holm oak survival is more influenced by field conditions than by the quality of the stock from nurseries (being equivalent to different provenances in this work) (Palacios et al. 2009). Yet, other authors showed that Holm oak saplings (young trees) from drier provenances were more resistant to drought, showing higher survival and post-drought growth (Andivia et al. 2018). In the short time span of this study, for one-year old seedlings, climatic provenance did not affect survival. However, we did not assess the effect of provenance on Holm oak survival in the long term, which could have shown different results. In the future, it would be interesting to study Holm oak growth and physiological status of the different provenances under contrasting climatic field conditions. The seedlings monitored for survival were the ones resulting from the germination trials, sometimes in small number. To further support our results, it would be helpful to have a consistently higher number of replicates, since the several provenances germinated differently.

Final Remarks

With this study it was possible to understand the main limiting factors for Holm oak performance, namely its germination and seedling establishment. Our findings provide guidelines that may help to increase Holm oak (re)afforestation success and may possibly contribute to better understand Holm oak natural regeneration patterns.

Climatic provenance is important for Holm oak acorn size and germination – acorn from areas subject to climatic harsher conditions germinate better. We suggest that this knowledge can be applied in the selection on propagules for (re)afforestation efforts, to increase the availability of Holm oak seedlings.

Holm oak seedling survival is severely constrained by climatic growing conditions, particularly during the summer drought period, dropping dramatically in drier and more exposed areas. Thus planning (re)afforestation efforts at a local spatial scale is key to their cost-effectiveness. On one hand it is important to map areas with less favorable climatic conditions that will need additional support, e.g. improving water availability to Holm oak seedlings, to ensure their survival. On the other hand, by mapping key (favorable) areas for Holm oak regeneration and establishment, stakeholders can allocate funds in a more informed way, prioritizing areas for (re)afforestation or changing land use, in a more efficient way to reverse *Montado* declining trends and to combat dryland desertification.

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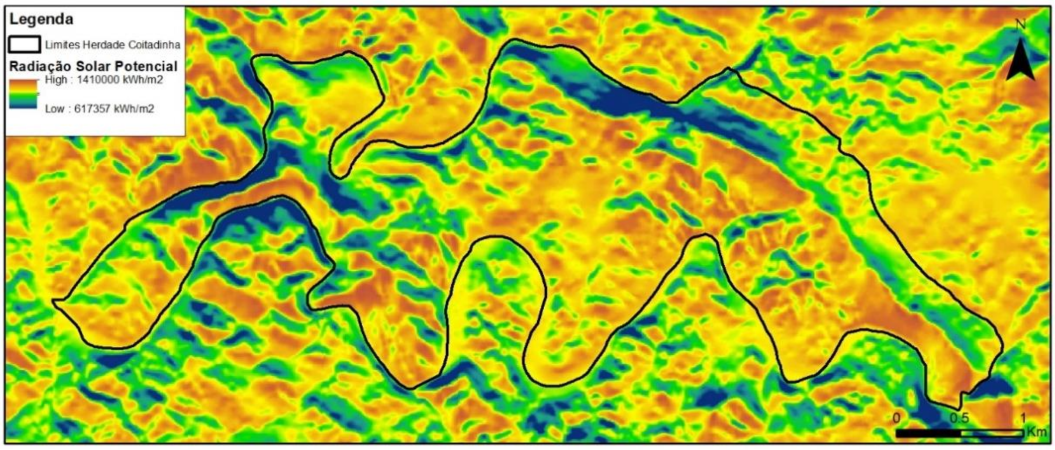
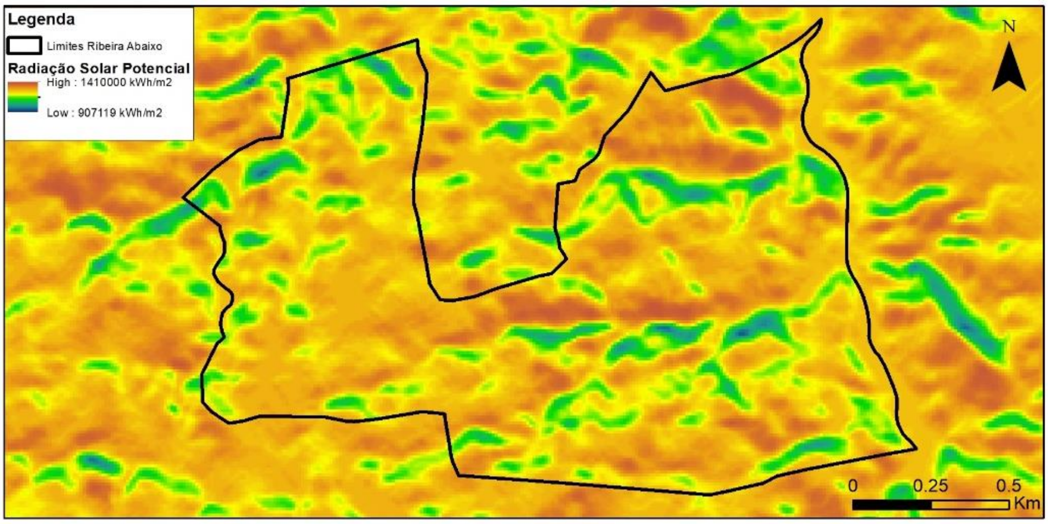
Appendix I – Potential Solar Radiation Maps

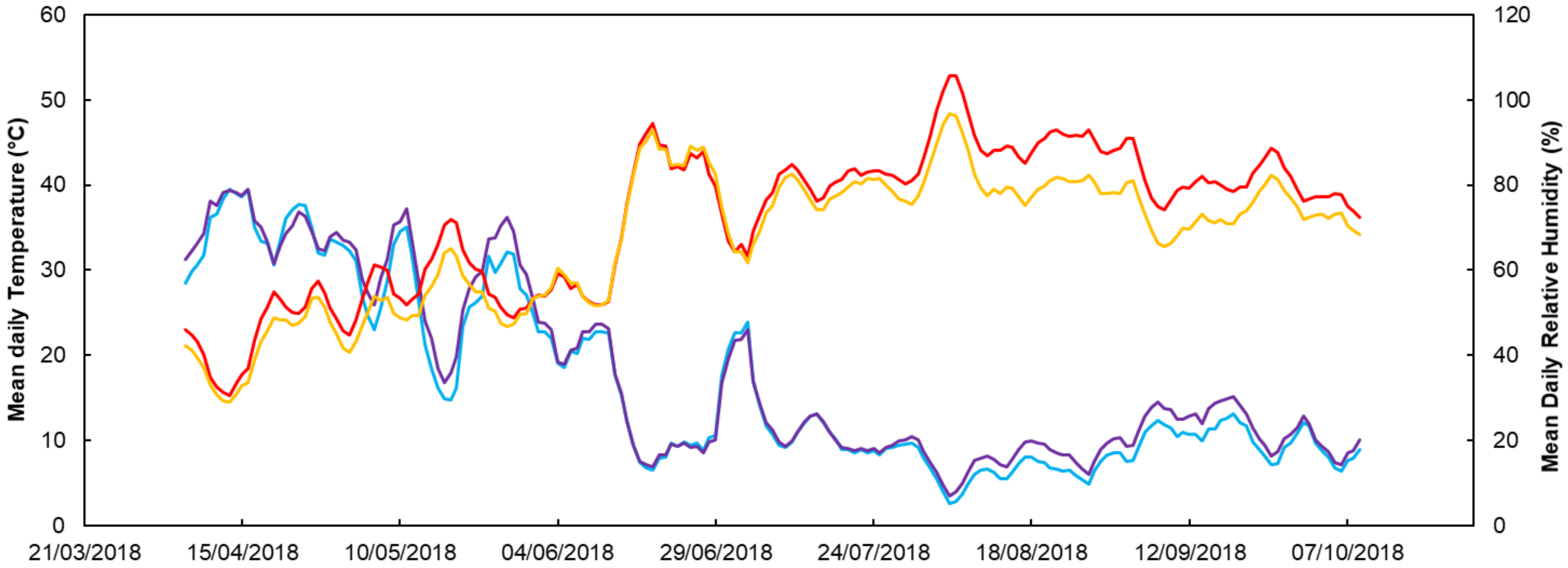


Supplementary Figure 1. Map of the drier site (Herdade da Coitadinha) with potential solar radiation that reaches the ground during a year represented.

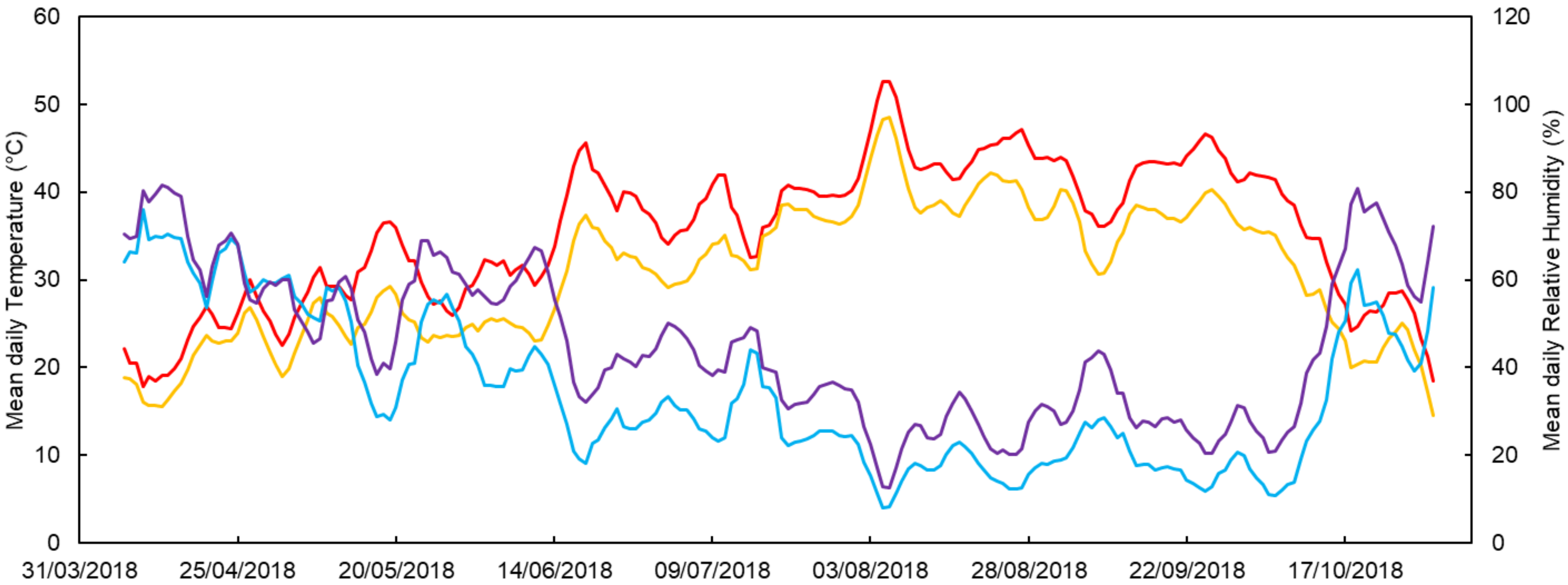


Supplementary Figure 2. Map of the wetter site (Herdade da Ribeira Abaixo) with potential solar radiation that reaches the ground during a year represented.

Appendix II – Environmental Characterization of Contrasting PSR Areas

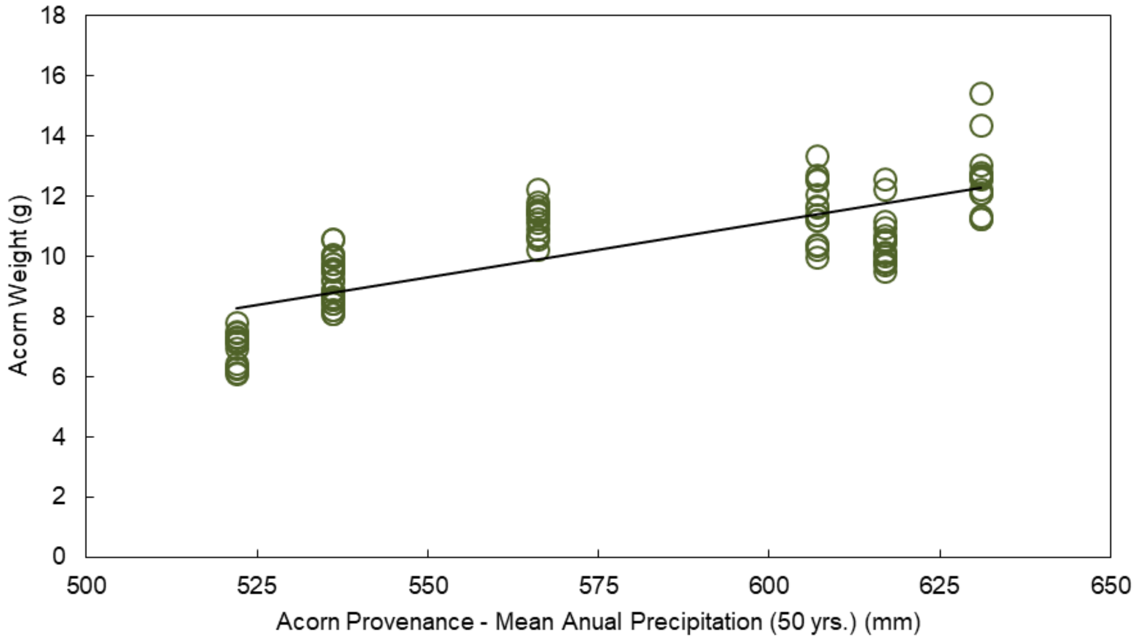


Supplementary Figure 3. Climate characterization of the drier site (Herdade da Coitadinha) at solar midday (14h00) in mean of 5 days: Red – mean temperature of high PSR slope; Yellow - mean temperature of low PSR slope; Blue – mean relative humidity of high PSR slope; Purple – mean relative humidity of low PSR slope. (N = 3)

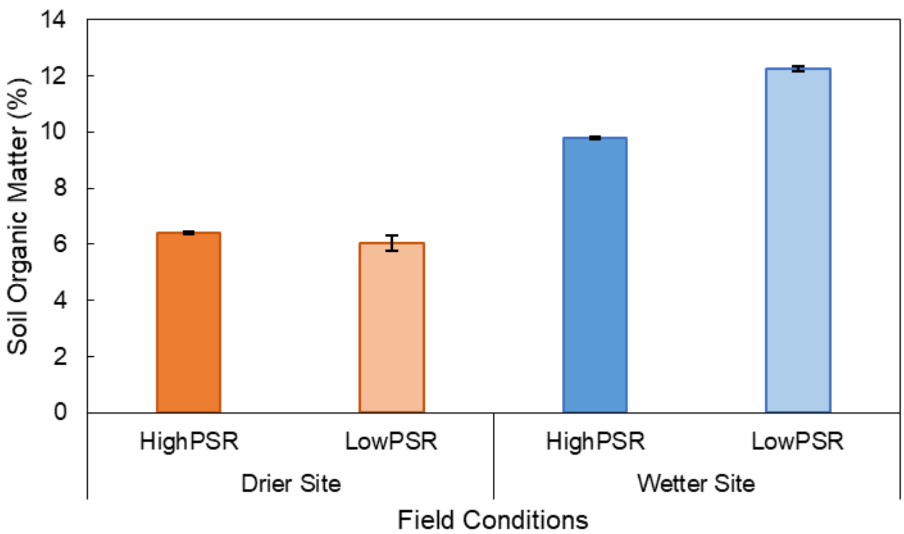


Supplementary Figure 4. Climate characterization of the wetter site (Herdade da Ribeira Abaixo) at solar midday (14h00) in mean of 5 days: Red – mean temperature of high PSR slope; Yellow - mean temperature of low PSR slope; Blue – mean relative humidity of high PSR slope; Purple – mean relative humidity of low PSR slope. (N = 3)

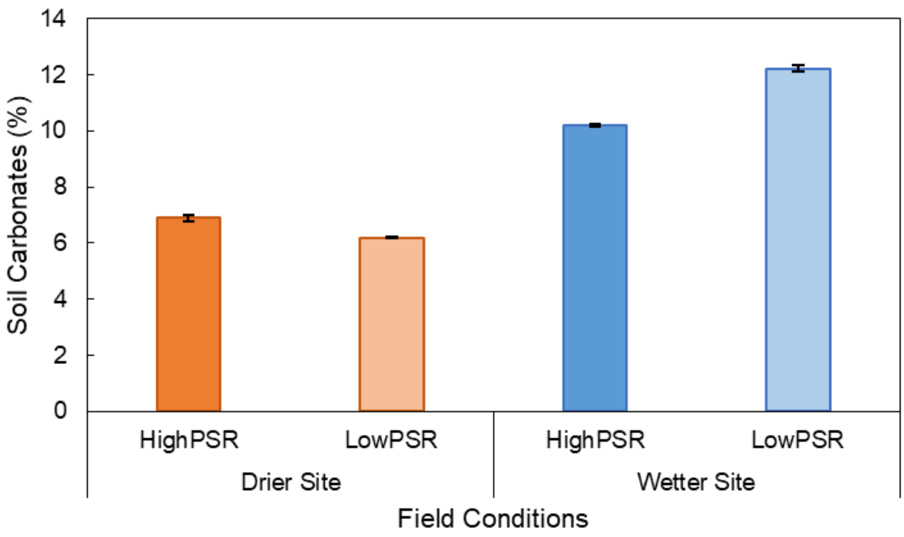
Appendix III – Additional Data



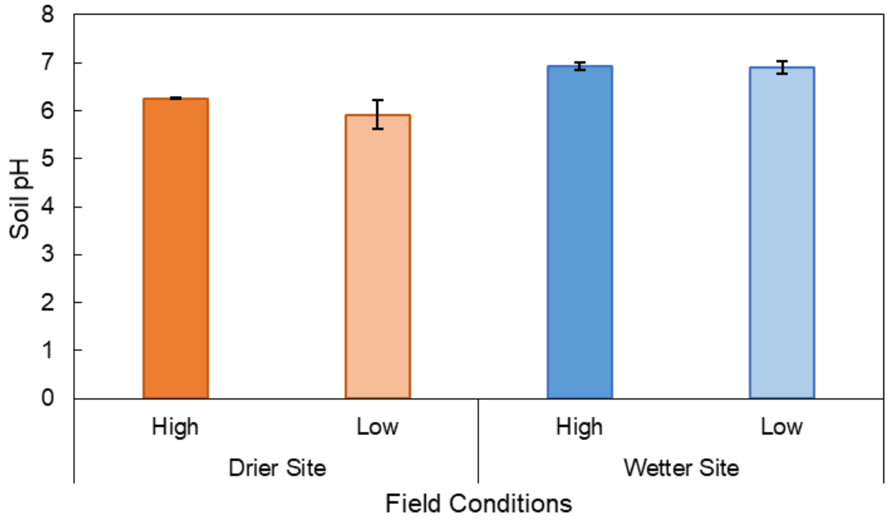
Supplementary Figure 5. Weight variation of acorns collected along the macroclimate gradient (different macroclimate provenance), based on mean annual precipitation; acorn composite samples (N = 15) from 6 sites, collected in the fall of 2018. The line represents the linear fit of the model (p-value< 2.2 e^{-16}; R2=0.61)



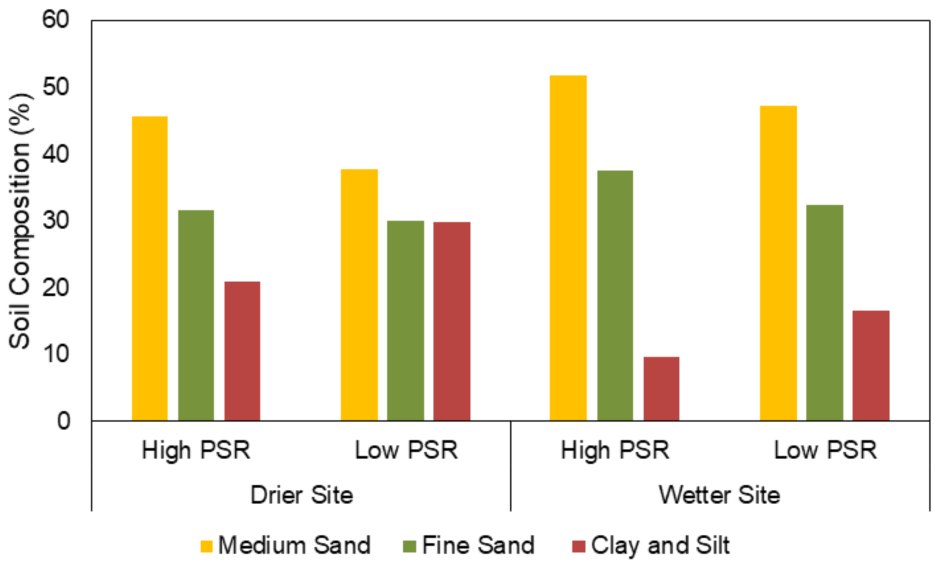
Supplementary Figure 6. Soil Organic Matter content of the different macro- and microclimatic areas where see/dlings were transplanted to the field (N = 3).



Supplementary Figure 7. Soil Carbonates content of the different macro- and microclimatic areas where seedlings were transplanted to the field (N = 3).



Supplementary Figure 8. Soil pH of the different macro- and microclimatic areas where seedlings were transplanted to the field (N = 3).



Supplementary Figure 9. Soil particle composition (< 2mm) of the different macro- and microclimatic areas where seedlings were transplanted to the field.

Appendix IV – Supplementary Tables

Supplementary Table 1. Summary of models: AW – Acorn Weight; ASW – Acorn specific Weight; AG – Acorn Germination; MAP – Mean annual precipitation (50yrs..) of provenance; GS – Greenhouse survival; Levels of significance are represented in the followings: "***" - p ≤ 0.001; "**"- p ≤0.010; "*" - p ≤ 0.050.; "." - p ≤ 0.100

Response variable	Predictors	Estimate	Significance	R2
AW (Dry year)	MAP	$-7.675e^{-01}$	***	0.5843
AW (Normal year)	MAP	$-4.462e^{-01}$	***	0.1934
AW (Normal year)	Prd	-0.05561	.	0.0600
AG (Dry year)	MAP	+38.1312	***	0.1012
	MAP^2	-38.2701	***	
AG (Normal year)	MAP	-0.5633	**	0.0528
AG (Normal year)	AW	+0.6584	**	0.0685
AG (Normal year)	ASW	+0.8320	***	0.0943
GS (Dry year)	MAP	-0.1246	.	0.0026
GS (Normal year)	MAP	+60.91	ns	0.3900
AW15B (Normal year)	MAP	$+7.838e^{-01}$	***	0.6106

Supplementary Table 2. Spearman correlation of acorn biometric parameters and climatic variables, the predictors are coloured in green and the responses in light brown: MAP – Mean annual precipitation (50yrs.); AW – Acorn Weight; AL – Acorn Length; AD – Acorn Diameter; AV – Acorn Volume; ASW – Acorn Specific weight. Levels of significance are represented in the followings: "***" - p-value ≤ 0.001; "**"- p-value ≤ 0.010; "*" - p-value ≤ 0.050.; " " - p-value > 0.50.

	MAP	AW	AL	AD	AV
AW	-0.83***				
AL	-0.67***	0.84***			
AD	-0.75***	0.89***	0.65***		
AV	-0.75***	0.93***	0.79***	0.97***	
ASW	-0.23*	0.25*	0.11	-0.05	-0.05

Supplementary Table 3. Spearman correlation of seedling field survival, the predictors are coloured in green and the responses in light brown: MAPc - Mean annual precipitation (50yrs.) to which the seedlings were transplanted; MAPp – Mean annual Precipitation (50yrs.) of seedling provenances; PSRd – Mean Potential Solar radiation of the area to which the seedlings were transplanted ; SOM – Soil organic matter; SOM sd – Soil organic matter standard deviation; SC – Soil carbonates; SC sd – Soil carbonates standard deviation; SpH – Soil pH; SpH sd – Soil pH standard deviation; MS – Medium sand percentage in the soil; FiS – Fine Sand percentage in the soil; CS – Clay and Silt percentage on the soil. Levels of significance are represented in the followings: "***" - p-value ≤ 0.001; "**"- p-value ≤ 0.010; "*" - p-value ≤ 0.050.; " " - p-value > 0.50.

	FS	MAPc	MAPp	PSRd	SOM	SOM sd	SC	SC sd	SpH	SpH sd	MS	FiS	CS	R
MAPc	0.51***													
MAPp	0.01	0.01												
PSRd	-0.35***	0.04	0.03											
SOM	0.45***	0.89***	0	-0.19*										
SOM sd	0.29***	-0.24**	-0.02	-0.75***	-0.29***									
SC	0.45***	0.89***	0	-0.19*	1.00***	-0.29***								
SC sd	0.20*	0.42***	-0.01	-0.41***	0.78***	-0.29***	0.78***							
SpH	0.26**	0.89***	0.02	0.44***	0.78***	-0.63***	0.78***	0.35***						
SpH sd	0.40***	0.01	-0.01	-0.60***	-0.16	0.94***	-0.16	-0.38***	-0.38***					
MS	0.26**	0.89***	0.02	0.44***	0.78***	-0.63***	0.78***	0.35***	1.00***	-0.38***				
FiS	0.26**	0.89***	0.02	0.44***	0.78***	-0.63***	0.78***	0.35***	1.00***	-0.38***	1.00***			
CS	-0.26**	-0.89***	-0.02	-0.44***	-0.78***	0.63***	-0.78***	-0.35***	-1.00***	0.38***	-1.00***	-1.00***		
R	-0.35***	0.04	0.03	1.00***	-0.19*	-0.75***	-0.19*	-0.41***	0.44***	-0.60***	0.44***	0.44***	-0.44***	
NR	0.35***	-0.04	-0.03	-1.00***	0.19*	0.75***	0.19*	0.41***	-0.44***	0.60***	-0.44***	-0.44***	0.44***	-1.00***

Supplementary Table 4. Spearman correlation of acorn production, the predictors are coloured in green and the responses in light brown: A_PSR- Annual PSR; J_PSR – January PSR; MAP – Mean annual precipitation (50yrs.); DAP cm – Breast height diameter; H – Tree Height; A/m^2 av – average of acorn per m^2; A/m^2 sd – standard deviation of acorns per m^2; BW15 –15 biggest acorns weight; BW15sd – 15 biggest acorns weight standard deviation; BV15 - 15 biggest acorns volume; BV15 sd – 15 biggest acorns volume standard deviation, SW – sown acorn weight; SW sd – sown acorn weight standard deviation, SV – sown acorn volume; SV sd – sown acorn volume standard deviation; GT – germination per tree; GMi – Germination of different microclimatic provenances; GMa – Germination different macroclimatic provenances. Levels of significance are represented in the followings: “***” - p-value ≤ 0.001; “**”- p-value ≤ 0.010; “*” - p-value ≤ 0.050.; “ “ - p-value > 0.50.

	A_PSR	J_PSR	MAP	MAP^2	DAP.cm	H	CA m^2	A/m^2 av	A/m^2 sd	BiW 15	BiW 15 sd	BiV 15	BiV 15 sd	SoW	SoW sd	SoV	SoV sd	GT	Gmi
J_PSR	0.99 ***																		
MAP	-0.58 ***	-0.54 **																	
MAP^2	-0.58 ***	-0.54 **	1.00 ***																
DAP.cm	0.06	0.05	0.06	0.06															
H	0.19	0.2	0.16	0.16	0.08														
CA m^2	-0.12	-0.15	0.21	0.21	0.36	0.39 *													
A/m^2 av	-0.24	-0.25	-0.21	-0.21	0.11	-0.26	-0.18												
A/m^2 sd	-0.21	-0.23	-0.26	-0.26	0.03	-0.28	-0.21	0.94 ***											
BiW 15	-0.17	-0.18	0.41 *	0.41 *	0	0.24	0.16	-0.35	-0.49 **										
BiW 15 sd	-0.33	-0.38 *	0.07	0.07	-0.3	-0.07	0.1	-0.08	-0.08	0.27									
BiV 15	-0.22	-0.22	0.44 *	0.44 *	0.02	0.25	0.24	-0.37*	-0.49 **	0.98 ***	0.3								
BiV 15 sd	SD	-0.28	0.1	0.1	-0.31	-0.05	0.11	-0.17	-0.15	0.26	0.92 ***	0.31							
SoW	0.26	0.28	-0.40 *	-0.40 *	-0.23	0.09	-0.18	-0.19	-0.28	0.49 *	0.15	0.42 *	0.13						
SoW sd	-0.32	-0.36	0.34	0.34	-0.35	-0.06	-0.04	-0.09	-0.1	0.60 **	0.45 *	0.56 **	0.44 *	0.36					
SoV	0.11	0.12	-0.16	-0.16	-0.26	0.12	-0.1	-0.26	-0.29	0.62 **	0.29	0.58 **	0.25	0.94 ***	0.53 **				
SoV sd	-0.27	-0.27	0.32	0.32	-0.42 *	-0.21	-0.09	-0.18	-0.13	0.42 *	0.45 *	0.43 *	0.53**	0.33	0.86 ***	0.51 *			
GT	0.38	0.42 *	-0.44 *	-0.44 *	-0.01	-0.13	-0.35	0.02	-0.07	-	-	-	-	0.61 **	-0.09	0.45 *	-0.03		
GMi	0.53 **	0.53 **	-0.79 ***	-0.79 ***	0	0.06	-0.29	0.26	0.22	-	-	-	-	0.60 **	-0.22	0.38	-0.28	0.59 **	
GMa	0.77 ***	0.78 ***	-0.72 ***	-0.72 ***	-0.09	0.14	-0.36 *	-0.16	-0.1	-	-	-	-	0.51 **	-0.23	0.32	-0.18	0.60 **	0.81 ***